

Madagascar and Indian Ocean Sipuncula

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Résumé. — Une collection de plus de 4 000 Sipunculides, représentant 54 espèces appartenant à 10 genres, est décrite. Les récoltes furent faites par de nombreux scientifiques lors de diverses campagnes océanographiques de 1960 à 1977. La plupart de ces récoltes proviennent de Madagascar et des eaux environnantes ; quelques-unes ont été réalisées dans l'océan Pacifique Ouest et quelques autres dans des régions intermédiaires. Cinq nouvelles espèces sont décrites (*Golfingia liochros*, *G. pectinatoida*, *Phascolion megaethi*, *Aspidosiphon thomassini* et *A. ochrus*). *Siphonosoma carolinense* est mis en synonymie de *S. cumanense*. *Phascolion africanum* est ramené à une sous-espèce de *P. strombi*. Des commentaires sont faits sur la morphologie de la plupart des espèces, et, surtout, des précisions nouvelles importantes sont faites pour *Siphonosoma cumanense*, *Golfingia misakiana*, *G. rutilofusca*, *Aspidosiphon jukesii* et *Phascolosoma nigrescens*. Des observations sur la répartition biogéographique des espèces sont données ; 10 espèces (6 *Aspidosiphon*, 2 *Phascolion*, et 2 *Themiste*) provenant d'aires très différentes de celles d'où elles étaient connues antérieurement sont recensées.

Abstract. — A collection of over 4000 sipunculans representing 54 species in 10 genera is described. The collections were made by numerous individuals and ships during the 1960's and early 1970's, most coming from Madagascar and surrounding waters ; a few from the western Pacific Ocean ; and some from intervening regions. Five new species are described (*Golfingia liochros*, *G. pectinatoida*, *Phascolion megaethi*, *Aspidosiphon thomassini*, and *A. ochrus*). *Siphonosoma carolinense* is submerged as a junior synonym of *S. cumanense*. *Phascolion africanum* is reduced to a subspecies of *P. strombi*. Morphological commentary is provided on most species but significant new information is offered for *Siphonosoma cumanense*, *Golfingia misakiana*, *G. rutilofusca*, *Aspidosiphon jukesii*, and *Phascolosoma nigrescens*. Zoogeographical observations are presented ; ten species (six *Aspidosiphon*, two *Phascolion*, and two *Themiste*) are herein reported from areas significantly different from their earlier known ranges.

INTRODUCTION

The information presented in this paper is based on material collected by numerous persons over several years time. The largest single collection was made by Dr. B. A. THOMASSIN, Station marine d'Endoume (SME) et Centre d'Océanographie, Marseille, in the coral reef complexes of the region of Tuléar (mainly on the "Grand Récif" barrier reef and lagoon, off Tuléar) and on the fringing reefs around Nosy Bé, S.W. and N.W. Madagascar (see THOMASSIN, 1969, 1971, 1973). P. GALENON (SME) studying samples made by the last researcher (BT) on the Tuléar coral reef boulder tracts also contributed some material from this region (see GALENON, 1977). Dr. R. PLANTE (SME) provided us with some subtidal

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collections in the Nosy Bé area. The remainder of the collections were made during the International Indian Ocean Expedition (1963-1964) and processed by the Smithsonian Oceanographic Sorting Center (SOSC). These were collected by several vessels (especially the "Anton Bruun" and "Te Vega") and persons. The funding for the U.S. program in biology of the IIOE was provided by the U.S. National Science Foundation.

There is a large body of literature on the Indian Ocean sipunculan fauna. HALDER (1975) and the monograph by STEPHEN & EDMONDS (1972) contain these references. The fauna of Madagascar was most recently reviewed by CUTLER (1965).

The 54 species included in this report, representing 10 of the 14 genera, are listed in table 1 along with a notation on their zoogeography. Five species new to science are described and named; three others are described but not named. Complete descriptions of the established species are not presented but can be found in STEPHEN & EDMONDS (1972). Table 1 shows that nine species are represented by more than 100 specimens, nine by 20-100, 14 by 10-19, and 22 by less than 10 specimens. Ten of the 46 established species are reported from regions significantly outside their previously known range, while 23 are reported from new localities but generally within their normal range. Important new information is presented for a few species where morphological studies of numerous specimens was productive.

There is one noteworthy example of how luck, fate, or the stars sometimes plays a role in science. "Anton Bruun" Sta. 407 I off north-western Madagascar contained five species from four different genera. At first we thought there was some mistake as the gear listed from this station was a hand line. After checking, it turns out that someone using a hand line, hooked a 66 pound head of coral from 58 m of water and hauled it up; a particularly fortuitous incident. The really interesting feature is the striking similarity between this station and one made on the other side of the ocean on the Coeas-Keeling Islands (Sta. B-5). This was in a lagoon off Direction Island in 10-20 feet of water with large *Porites* heads. Four of the five species found at 407 I were also found here. A second Coeas-Keeling station (B-3) contained two of these four (*Lithacrosiphon maldivensis* and *Aspidosiphon steenstrupi*) and these two are not found anywhere else in these collections. A third species (*Aspidosiphon ochrus*) is a new species and found at only two other localities. The fourth species common to the two areas is *Cloeosiphon aspergillus*.

The biological similarity between these two widely spaced areas is intriguing. The apparent absence of these species in the intervening space is also curious and the luck of finding this one head of coral certainly should make all zoogeographers once again qualify their conclusions with a clear message that what we know is not necessarily what is.

In the systematics section most of THOMASSIN'S stations (BT) are from the Tuléar and Nosy Bé (*Enhalus acoroides* seagrass beds) regions or from the Tiahura reef complex, Moorea Island, French Polynesia¹ (Moorea BT); exceptions will be noted. P. GALENON'S (PG) are from the greater Tuléar region and PLANTE'S (RP) are from within 80 km of Nosy Bé Island. The IIOE station data is included with each species. We have also included a few other Pacific Ocean records: collections made by M. A. CHARTOCK, Univ. Southern California, Los Angeles, on Eniwetok atoll, Marshall I.

1. Study done in joint research program with the Antenne of the Paris Muséum-ÉPHÉ of Tahiti, in July 1973.

Table 1. Species included in this report. ^(a)Symbols for zoogeographical notation: A- These records consistent with earlier ones; B- From new localities but previously reported from the Indo-West Pacific; C- Significant extensions of known range; X- No comparative data.

Species	Number of stations	Number of specimens	Zoogeographical notation (a)	Species	Number of stations	Number of specimens	Zoogeographical notation (a)
SIPUNCULIDAE				ASPIDOSIPHONIDAE			
<i>Sipunculus</i>				<i>Aspidosiphon</i>			
<i>S. aequabilis</i>	1	1	A	(<i>Aspidosiphon</i> s.s.)			
<i>S. indicus</i>	3	5	A	<i>A. elegans</i>	4	15	B
<i>S. longipapillosus</i>	4	12	A	<i>A. exhaustus</i>	6	17	C
<i>S. norvegicus</i>	2	3	A	<i>A. jukesii</i>	68	503	B
<i>S. nudus</i>	1	1	A	<i>A. kovaleskii</i>	4	13	B
<i>S. titubans</i>	7	14	B	<i>A. venabulus</i>	7	17	C
<i>Siphonosoma</i>				<i>A. nimii</i>			
(<i>Damosiphon</i>)				<i>A. thomassini</i> sp. nov.	63	241	X
<i>S. rumanense</i>	123	408	B	(<i>Paraspidosiphon</i>)			
(<i>Hesperosiphon</i>)				<i>A. angulatus</i>	2	19	C
<i>S. vastum</i>	4	7	B	<i>A. klunzingeri</i>	8	16	C
(<i>Siphonosoma</i> s.s.)				<i>A. speculator</i>	8	22	C
<i>S. australe</i>	6	25	A	<i>A. steenstrupii</i>	3	14	A
GOLFINGIIDAE				<i>A. truncatus</i>			
<i>Golfingia</i>				<i>A. cochrus</i> sp. nov.			
(<i>Golfingia</i> s.s.)				<i>Litharosiphon</i>			
<i>G. ruminata</i>	2	3	A	<i>L. cristatus</i>	1	1	B
<i>G. vulgaris</i>	1	1	B	<i>L. maldivensis</i>	3	9	B
<i>G. lichros</i> sp. nov.	8	8	X	<i>Cleosiphon</i>			
<i>G. pectinoida</i> sp. nov.	23	130	X	<i>C. aspergillus</i>	36	420	A
(<i>Golfingiella</i>)				<i>Centrosiphon</i>			
<i>G. pudica</i>	1	6	B	<i>C. species</i>	3	3	X
(<i>Fisherana</i>)				PHASCOLOSOMATIDAE			
<i>G. misakiana</i>	85	535	B	<i>Phascolosoma</i>			
(<i>Mitosiphon</i>)				(Satonus)			
<i>G. trichocephala</i>	77	311	B	<i>P. pectinatum</i>	1	1	B
(<i>Phascoloides</i>)				(Phascolosoma s.s.)			
<i>G. minuta</i>	1	59	A	<i>P. albolineatum</i>	2	26	B
<i>G. rutilofusca</i>	23	66	B	<i>P. agassizii</i>	2	3	B
<i>G. species</i>	3	10	X	<i>P. funafutiense</i>	3	21	B
<i>Phascolion</i>				<i>P. nigrescens</i>	58	180	B
<i>P. beklemischevi</i>	1	2	C	<i>P. pacificum</i>	18	49	B
<i>P. pharetratum</i>	6	8	C	<i>P. perlucens</i>	15	37	A
<i>P. strombi africanum</i>	8	12	B	<i>P. scolops</i>	49	227	B
<i>P. valdivae</i>	1	13	B				
<i>P. megaethi</i> sp. nov.	5	8	X	TOTAL OF SPECIMENS			
<i>P. species</i>	1	1	X			4 083	
<i>Themiste</i>							
<i>T. lageniformis</i>	2	18	A				
<i>T. liessa</i>	1	2	C				
<i>T. minor</i>	1	1	B				
<i>T. robertsoni</i>	5	21	C				

NOTE ADDED IN PRESS : In CUTLER, 1979, *Mitosiphon* and *Fisherana* are combined into *Apionsoma* and *Phascoloides* is changed to *Nephasoma*.

The habitat and ecological position of many of these species will be outlined in more detail in forthcoming publications of B. THOMASSIN¹.

In addition to those persons already named, we are indebted to all the many people who made these collections and to the staff of the SOSOC for processing much of it. Most of this work was done at Duke University Marine Laboratory while on sabbatical leave from Utica College. The artwork was done by Mr. Henry IWANICKI, Utica.

***Sipunculus aequibilis* Sluiter, 1902**

HIOE Sta. 17, 1 spec.; 3/21/63; 7°38' N, 97°08' E; 510 m; Strait of Malacca.

This single specimen has 21-23 longitudinal muscle bands and free nephridia which open slightly anterior to the anus between bands 4 and 5. The retractor muscles are slender with the ventral pair originating from band 3 and the dorsals from bands 8 and 9. In STEPHEN & EDMONDS (1972 : 25) the statement is made that the introvert is "... about one eighth as long as the trunk". SLUITER (1902) described this as being one fourth the trunk length. This worm has a 55 mm trunk and a 14 mm introvert.

DISTRIBUTION. — This record fits in well with previous ones as a deeper water member of this genus. It has been recorded from the Mediterranean Sea, Gulf of Aden, Laccadive Island, Bay of Bengal and Indonesia from depths of 26-1686 m, most being several hundred meters. This species appears to be restricted to deep water and with the exception of the Mediterranean Sea record is, so far, an Indian Ocean form.

***Sipunculus indicus* Peters, 1850**

HIOE Sta. JR-8; 3 spec.; 12/23/63; 13°24' S, 48°22' E; 1 m; Nosy Bé.
Tuléar BT Sta. : Port Tuléar; 1 spec.; 839, 1 spec. Lagoonal bottoms and littoral sand banks.

The three worms from Sta. JR-8 and the one from Sta. 839 are in good, "normal" condition and are easily assigned to this taxon. The one from Sta. Port Tuléar had dried out at some point and the internal organs were destroyed. It does have 40-41 longitudinal muscle bands and is placed here with some reservation. The fishermen in the Tuléar region use this species for bait as has been recorded elsewhere (CUTLER, 1965).

DISTRIBUTION. — This has been previously recorded from Madagascar as well as from neighboring east and south Africa through the Indian Ocean, the South China Sea, and several West Pacific Islands. It is a shallow water species and a representative of the Indo-West Pacific shallow water province.

1. For these results see : B. A. THOMASSIN (1978), Les peuplements des sédiments coralliens de la région de Tuléar (S. W. de Madagascar). Leur insertion dans le contexte côtier indo-pacifique. Thèse Doct. ès-Sci., Univ. Aix-Marseille II, 22 avril 1978, Archives originales du CNRS, n° A.O. 11.581 : 494 p. multigr., 180 tabl., 209 fig. + Annexe méthodologique : 101 p., Annexe faunistique : 302 p.

Sipunculus longipapillosus Murina, 1968

IIOE Sta. 243B; 1 spec.; 11/28/63; 24°54' N, 61°48' E; 107 m; S. of Karachi. — Sta. 254B; 2 spec.; 11/30/63; 25°35' N, 57°09' E; 256 m; Gulf of Oman. — Sta. 255A; 1 spec.; 11/30/63; 25°48' N, 57° 07' E; 93 m; Gulf of Oman. — Sta. 261A; 8 spec.; 12/01/63; 25°53' N, 56°53' E; 99 m; Gulf of Oman.

This species with the girdle of long papillae in the mid-trunk region is quite distinctive. These animals with 24-29 longitudinal muscle bands, spindle and fastening muscles, and much connective tissue anchoring the gut coil to the body wall, ranged in trunk length from 35-102 mm. The papillated region of the trunk ranged from 30-75 % of the trunk, most covering about 50 %.

DISTRIBUTION. — The two previous records of this species are from this same general area, the Red Sea at 368 m and the Gulf of Oman at 199 m. This would seem to be a very localized species along the edge of the photic zone in the northwestern part of the Indian Ocean. However, there is a recent unpublished record from the Gulf of Mexico off Panama City, Florida.

Addendum : Since completing this manuscript, two additional specimens were sent to us by Dr. H. ZIBROWIUS (SME) from the southern Red Sea collected during the Suidit Campagne Same-rouad N.O. "Suroit" on 30/1/77. The station was at 14°44' N, 42°27' E at depths of 350-700 m. They are both in good condition and fit the above comments.

Sipunculus norvegicus Danielssen, 1868

IIOE Sta. 409E; 1 spec.; 10/10/64; 16°11' S, 43°42' E; 62 m; NW Majunga, Madagascar. — Sta. AB19; 2 spec.; 3/23/63; 8°30' N, 97°58' E; 42 m; SW of Sumatra.

These three worms exhibit the typical 22-24 longitudinal muscle bands, nephridia opening a little anterior to the anus, and unattached for most of their length. The ventral retractor muscles originate from longitudinal muscle bands 2-4 and the dorsals from 9-10.

DISTRIBUTION. — This species is common in cooler waters of the North Atlantic as far south as the Carolinas on the western side and West Africa and Cape Verde Islands in the east. These records fit in with scattered reports from the Suez Canal, East Africa and Madagascar, over to Indonesian waters, Loyalty Islands and Hawaii and suggest it is more widely distributed. Most of the records are from 50-1500 meters.

Sipunculus nudus Linnaeus, 1766

Nosy Bé BT Sta. 557; 1 spec.; *Enhalus acoroides* patch.

This pinkish grey specimen measured 39 × 10 mm but had its posterior end amputated during collection so is incomplete. The surface shows the typical *Sipunculus* confi-

guration. The circular muscles are well defined and 33 longitudinal muscle bands are present.

DISTRIBUTION. — This is the nearest thing to a cosmopolitan species in this genus having been reported from shallow subtidal waters in the tropical and sub tropical areas of all the world's oceans including the Mediterranean and Red Seas. A single report (HALDER, 1975 : 55) from the Laccadive Islands at 2 308 m seems out of the norm for this species.

Sipunculus titubans Selenka, de Man & Bulow, 1883

Tuléar Bt Sta. : 777A, 1 spec. ; 788, 1 ; 790, 1 ; D30, 1 (damaged).
Moorea BT Sta. : 19, 2 spec. ; 27, 2 ; 29, 4.

As STEPHEN & EDMONDS (1972 : 38) point out, this is a confusing species. These 17-50 mm specimens have from 24-30 longitudinal muscle bands and fit the description fairly well. In several, the nephridia are unattached, in one they are attached for about 1/4 their length, and in one, they are attached for 1/2 their length as they are described. The position of the anus and the nephridiopores varies from both being at the same level, to the anus being 2 mm anterior to the nephridiopores. In the animal from Sta. 790 the circular muscles are more prominent than the longitudinal and the worm from Sta. 788 has a cluster of several large (4 mm long in a 50 mm worm) finger-shaped outgrowths from its rectum.

The eight Pacific Ocean worms all had 24-25 longitudinal muscle bands and could easily be confused with *S. norvegicus*.

DISTRIBUTION. — This species appears in the Caribbean, off the Canary and Cape Verde Islands and tropical West African waters, then off Zanzibar, Madagascar, Siam (Thailand), in the East China Sea and the Pacific coast of Costa Rica. These records support a construct of a shallow water, tropical species now absent from only the eastern Indian Ocean.

Siphonosoma (Damosiphon) cumanense (Keferstein, 1867)

Siphonosoma carolinense Fischer, 1928 : 138-140 ; STEPHEN & EDMONDS, 1972 : 44-46.
Siphonosoma novaepommeraniae Wesenberg-Lund, 1959.

IIOE Sta. : RU-2 ; 4 spec. ; 8/20/64 ; 25°50' S, 32°55' E ; 1 m ; Inhaca, Mozambique. — IIA 67-32 ; 1 spec. ; 8/5/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia. — HA 67-40 ; 4 spec. ; 7/10/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia.

Nosy Bé RP Sta. : 7, 1 spec. ; 10, 2 ; 12, 1. — BT Sta. : NSB 9, 1 spec. ; 552, 6 ; seagrass beds.
Tuléar PG Sta. : many on the outer boulder tracts of reefs. — BT Sta. : a lot, mainly in the sediments of the outer boulder tracts, the sandy bottoms of inner pools, the seagrass beds, on the barrier reef, few in lagoon bottoms, and in the littoral tidal flats with or without seagrass beds and mangrove.

This collection of 329 worms from a single population (Tuléar stations) provided a valuable analytical base for some troublesome points. As STEPHEN & EDMONDS (1972 : 44)

state : " The species in this subgroup are remarkably alike and it is possible that they are synonymous. " They proceeded to reduce six names down to three : *S. edule*, *S. cumanense* and *S. carolinense*. The first differing from the others due to a shorter introvert and the remaining two differentiated by a differing number of tentacles. The following comments are based on an analysis of 306 worms from Tuléar, four from Inhaea, some from Nosy Bé (CUTLER, 1965), and GEROULD's (1913) from Florida. The measurements taken were based on a subset of 45 entire worms ranging in size from 3-230 mm, many others had been damaged during the collection process and were incomplete.

Ratio of introvert to trunk length. Of the three species in this subgenus, *S. edule* reportedly has a trunk 8-14 times the length of the introvert, the other two having longer introverts. The trunks in this group ranged from 1.2-4.7 times the introvert length with a wide spread of values through the middle sized worms. EDMONDS' data from my Madagascar worms shows a higher slope with values ranging from 2.5-7 times the introvert length. The table in STEPHEN & EDMONDS (1972 : 47) has an error : it states millimeters where it means centimeters in the headings. At any rate, if the *S. edule* data is true, perhaps there is a real difference as none of these introverts were that short.

If one converts these measurements to determine what percentage of the total length is made up of introvert (i.e. if the trunk is 3 times the introvert length then the introvert

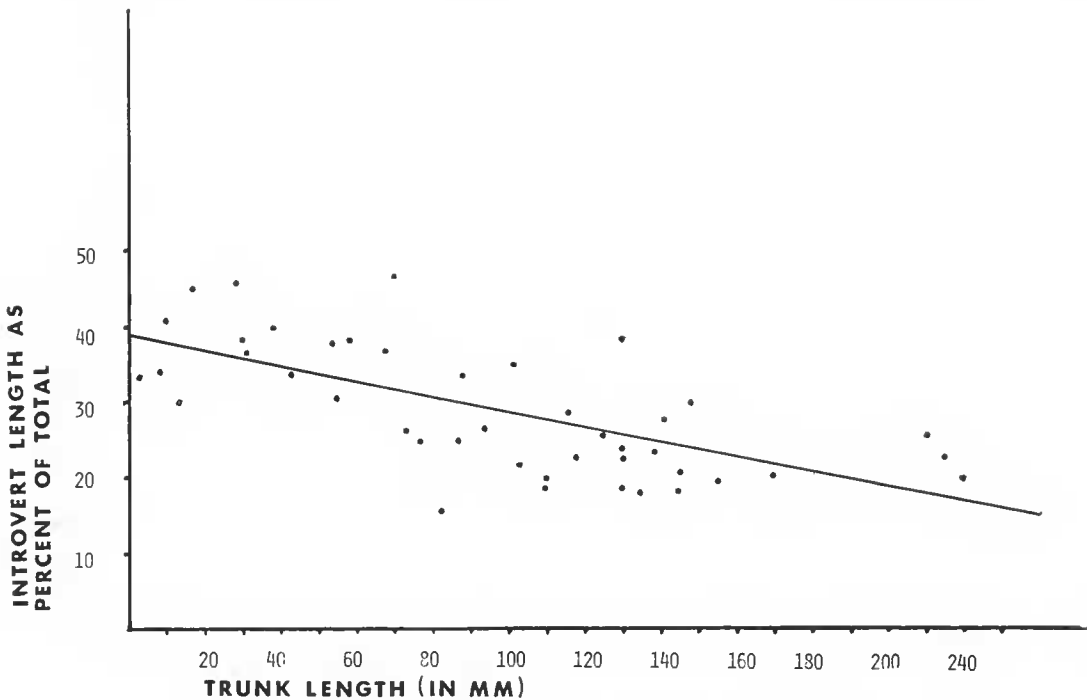


FIG. 1. — The relationship between trunk and introvert length in *Siphonosoma cumanense*. Simple linear regression ($Y = a + bx$), $a = 38.4$, $b = -0.13$.

is 25 % of the total) it becomes obvious that larger worms have proportionately smaller introverts (fig. 1). This would appear to be a clear example of allometric growth (a not uncommon biological phenomenon) where the trunk grows at a faster rate than the introvert.

Extrapolating from the data shown in figure 1 it is possible that large *S. cumanense* (over 250 mm trunk) would have an introvert small enough to approach the 7-11 % range reported for *S. edule*. The unanswered question then becomes : are *S. edule* only very large *S. cumanense* or *S. cumanense* with unusually short introverts ?

Tentacle number. *S. carolinense* differs from *S. cumanense* according to STEPHEN & EDMONDS (1972 : 44) by having 60-80 tentacles instead of 25-30. In this population we found it very difficult to make an accurate count of the tentacles, especially as most had retracted introverts. Also, there may be some confusion due to the bifurcated nature of these structures. We counted the tips, not the bases. The range we found was from 14-120, most between 25 and 45 with a spread of values in the middle sized worms. The smallest have the fewest and the largest have the most, very few having 60 or more (15-20 % of the sample).

Transverse dissepiments. Supposedly all the species of this subgenus have these sheets of connective tissue transversing the coelom. However, this is probably the most variable of the variables in these worms. They were not discernable in all worms, and when present, their number, distribution, strength, height, etc. were very different from one worm to the next and with no apparent relationship to size or state of contraction/relaxation. Sometimes strong, then weak ; high from the body wall, then low to it ; many, then few ; some spread over a wide area, then others restricted to a few short patches. In one 17 mm worm they were easier to see than in a 215 mm worm. Those with undiscernable dissepiments ranged in size from 3-110 mm. I suspect that in the past, other authors with few animals may well have overlooked these, and I seriously wonder about the logic of giving such a difficult and variable trait subgeneric value. Also, *S. novaeopommeraniae* is exactly like *S. cumanense* except it lacks the transverse dissepiments. WESENBERG-LUND (1959a) says they exist in her Mauritius forms of *S. novaeopommeraniae* and even draws them. Hers then should be considered *S. cumanense* and possibly FISCHER's (1926) should be here also.

Nephridia/anus relationship. Measurements were taken and in all cases the nephridia were anterior to the anus, from 1/2-7 mm. Again, the smallest have the least distance between them and the largest have the most, but in the middle range there is a large spread with most showing 1-3 mm space between the two openings.

Retractor origins. In all the specimens the ventral and dorsal retractor muscles came from the same anterior/posterior level.

Anastomosing. The anastomosing of the longitudinal muscle bands occurred only very rarely, perhaps 2-6 times in any one worm and more commonly in worms over 100 mm long. As a rule one has to look hard to find any.

In view of the above discussion, the minor differences between *S. cumanense* and *S. carolinense*, and the overlapping distribution, we suggest that *S. carolinense* be considered a junior synonym of *S. cumanense*.

DISTRIBUTION. — This common species has been previously reported from Madagascar, East and South Africa as well as several other Indian Ocean locations up into the Red Sea. It is found in Indo-China up to Japan and China and down to Australia to New Guinea and several West Pacific Islands. It also occurs in the western Atlantic from Florida to Venezuela. It seems to be absent from the eastern Atlantic and Pacific.

Siphonosoma (Hesperosiphon) vastum (Selenka, de Man & Bulow, 1883)

IIOE Sta. KA-9; 1 spec.; 11/18/64; 4°05' S, 39°14' E; 1 m; Mombassa, Kenya.

Tuléar BT Sta. 751A, 1 spec. — MC Sta. 12; 1 spec.; 8/28/70; 11°21' N, 162°22' E; 1 m; Eniwetok. — HA 67-40; 4 spec.; 7/10/67; 7°21' S, 72°28' E; 1 m; Diego Garcia.

In this subgenus there are only three species, all having fringes or club-shaped caecae on the rectum. The presence of rings of pale introvert hooks and numerous caecae easily distinguish this form. There are four retractor muscles and a posteriorly attached spindle muscle. Transverse dissepiments are lacking as are contractile vessel villi. The longitudinal musculature is arranged in 27-28 bands.

DISTRIBUTION. — This shallow water Indo-West Pacific form has been recorded several times from Mauritius through the Indian Ocean, Indonesia, Australia and several West Pacific Islands. This is the first record from any of these locations.

Siphonosoma (Siphonosoma) australe (Keferstein, 1865)

Tuléar BT Sta. : 3, 8 spec.; 5, 9; 7, 3; 8, 3; 9, 2; 673, 1 piece with hooks; littoral tidal flats without seagrass beds.

These 25 worms range in trunk length from 15-120 mm and as they have no dissepiments in the body cavity or numerous rectal caecae, easily fall into this subgenus. The large, pointed, spine-like hooks on the introvert and single rectal caecum characterize this well known species. The nature of the fixing muscle with three branches shows up very nicely.

DISTRIBUTION. — This is another Indo-West Pacific shallow water species having been recorded from Durban, Zanzibar, Madagascar, through India to Indonesia, Australia, New Zealand and a few West Pacific Islands.

Golfingia (Golfingia) muricaudata (Southern, 1913)

IIOE Sta. 369C; 1 spec.; 8/17/64; 23°48' S, 37°46' E; 2200 m; Mozambique Channel. — Sta. 370D; 2 spec.; 8/18/64; 24°28' S, 35°36' E; 880 m; Mozambique Channel.

These animals with four retractors and a short caudal appendage (2 mm in a 15 mm worm) are the same as found in the Atlantic Ocean (CUTLER, 1973). The worm from Sta. 369C had its introvert missing, but the others were intact and without hooks.

DISTRIBUTION. — This deep water species has been collected at widespread localities in the north Atlantic and Pacific Oceans including Hudson Bay, from the Atlantic coast of South America and Bouvet Island in the South Atlantic. This record confirms its presence in this southwest corner of the Indian Ocean. This is the closest thing to a bipolar species in this report as all the records have been outside the 20° north and south latitudes. These depths fit into the known vertical distribution of 450-3000 m.

***Golfingia (Golfingia) vulgaris* (de Blainville, 1827)**

IIOE Sta. 392K; 9/10/64; 29°19' S, 31°36' E; 38 m; off Durban OR. — 391C; 9/9/64; 29°29' S' 31°45' E; 86 m; (label confusion at SOSC) 1 specimen.

This worm shows the typical pale trunk with light brown pigmentation on both ends, much of it being covered with low, flat papillae or skin bodies which look like clear spots when viewed with transmitted light. Internally the normal arrangement of organs is found and the introvert hooks measure 80-90 μ m in height.

DISTRIBUTION. — This is an East Atlantic-Indian-West Pacific Ocean species with its density being highest off Europe and West Africa and through the Mediterranean with occasional reports through the Red Sea, Zanzibar but then skipping across to Malaya, East China Sea, Singapore, Australia and Japan with an Antarctic and Kurile-Kamohatka Trench record also. This is the most southerly record for this area.

***Golfingia (Golfingia) liochros* n. sp.**

Golfingia (Golfingia) n. sp. Cutler, 1977.

IIOE "Te Vega" Sta. 82 LH 10; 1 spec.; 11/6/63; 9°26' N, 97°54' E; 1 m; Thailand.
Tuléar BT Sta. : 634, 1 spec.; 654B, 1; 755, 1; 781A, 1; 782, 1; 797, 1; 801, 1. More frequently located in the sediments clogging the outer boulder tracts of the barrier reef; one time sampled in a seagrass bed.

These worms are the same as an unnamed *Golfingia (Golfingia)* from Mozambique partially described in CUTLER (1977). They have a striking external appearance: the trunk is smooth, slippery white or pink while most of the introvert and posterior end of the trunk are covered with densely packed, uniform sized, spheroid to digitiform, yellowish-orange papillae, giving these regions a granular look (fig. 2). When the introvert is retracted the papillated areas may look somewhat shield-like. The introvert, which is shorter than the trunk, becomes transparent at the distal end and bears scattered hooks measuring 40-120 μ m along their longest axis. One worm has its introvert completely extended and six tentacular lobes are discernable. The trunk dimensions are 5-19 mm long by 0.5-3 mm wide. The variations in color of the papillae in these worms may be due to different postmortem chemical environments. Those collected by the "Galathea" were brown, the Tuléar worms were pale orange and the "Te Vega" worm was off white. The smallest one from Sta. 654 has a transparent body wall and the papillae are only slight-

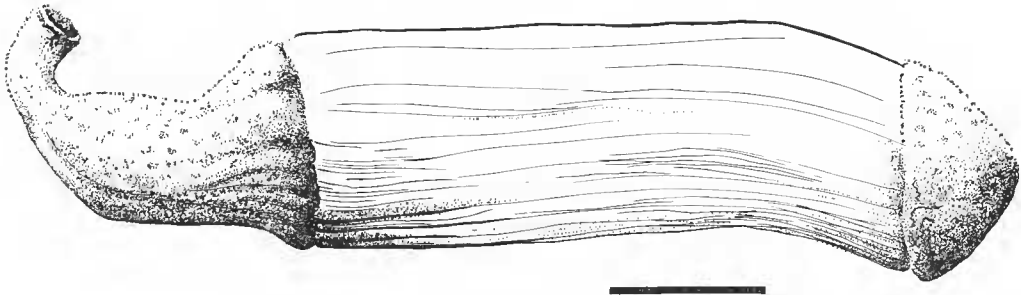


FIG. 2. — *Golfingia liochros* n. sp. Whole animal, introvert partially extended.
(Scale = 2 mm.)

ly pigmented. This is placed here with some reservations. The hooks follow the same trend i.e., those from the "Galathea" worm were dark, the Tuléar worms were paler and in the "Te Vega" worm the hooks were very light colored and almost clear.

Internally there are four retractor muscles. The ventral pair are three to four times the diameter of the dorsals and originate at about the middle of the trunk, while the finer dorsal pair originate half way between the middle of the trunk and the anus. The single lobed, tubular nephridia are free from the body wall, one third to one half the length of the trunk, and open at the level of the anus. The spindle muscle is present but not attached posteriorly. A single fixing muscle is present attaching the third gut coil to the body wall near the origin of the right dorsal retractor muscle. No rectal caecum was observed but along the contractile vessel, while it is still associated with the retractor muscles, are a few pale orange bubble-like swellings or vesicles; not villi. A pair of pigmented eyespots is present on the brain.

In this subgenus two species have been described with hooks, tentacles, "normal" retractor muscles, and an *Aspidosiphon*-like shield at both ends of the trunk: *G. sanderi* and *G. scutigera*. In addition to the different nature of the "shields" and position of the ventral retractor muscle origin, the well defined hooks not arranged in rows set this form apart from these other two. The name *liochros* was chosen from the Greek meaning smooth-skinned.

The type specimen has been deposited in Muséum national d'Histoire naturelle, Paris. Holotype: Cat. N° AH-411; BT Station 755; "Grand Récif", Tuléar, Madagascar.

DISTRIBUTION. — "Galathea" Sta. 214 off Beira, Mozambique, 20°10'S, 35°15' E at 380 m in clay, plus these records from Tuléar, Madagascar, and off Thailand.

***Golfingia* (*Golfingia*) *pectinatoida* n. sp.**

Tuléar BT Sta. : 124, 6 spec.; 236, 1; 256, 1; 259, 6; 654, 11; 654 B, 1; 751A, 3; 752, 2; 755, 13; 757, 11; 782, 6; 784, 18; 788, 13; 795, 2; 797, 3; 801, 22; 803, 1; 811, 5; 831, 1; 852, 1; 870, 1; 916, 4. Most of the specimens were collected in the sediments elogging the outer boulder tracts on the barrier reef; others samples are from sediments of the outer reef slope, reef flats and enclosed lagoon slope.
Moorea BT Sta. : 16, 1 spec.; 19, 2.

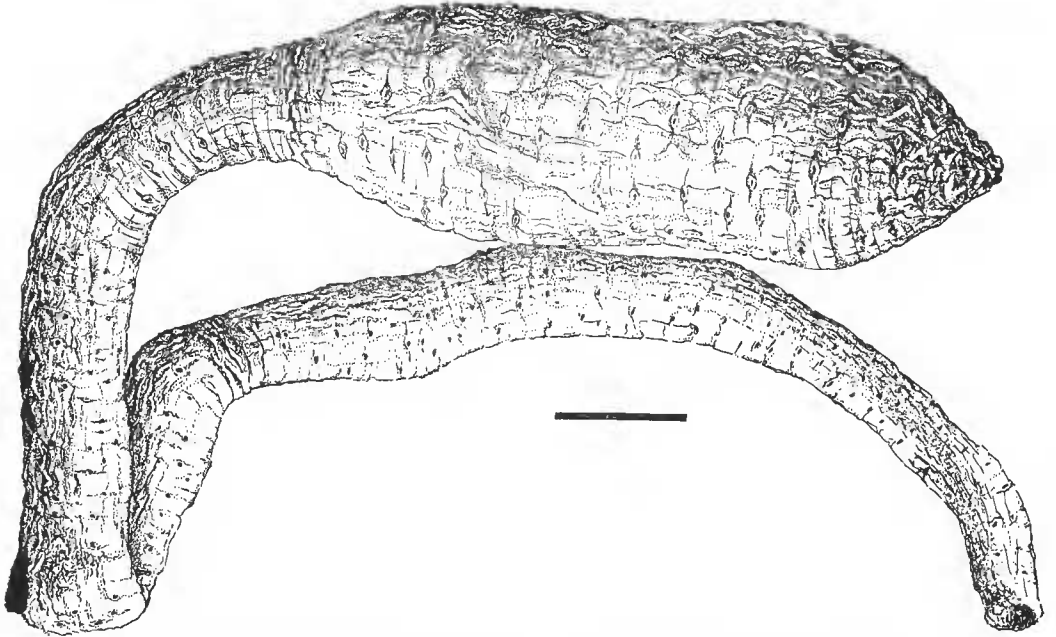


FIG. 3. — *Golfinzia pectinatoida* n. sp. External view. (Scale = 1 mm.)

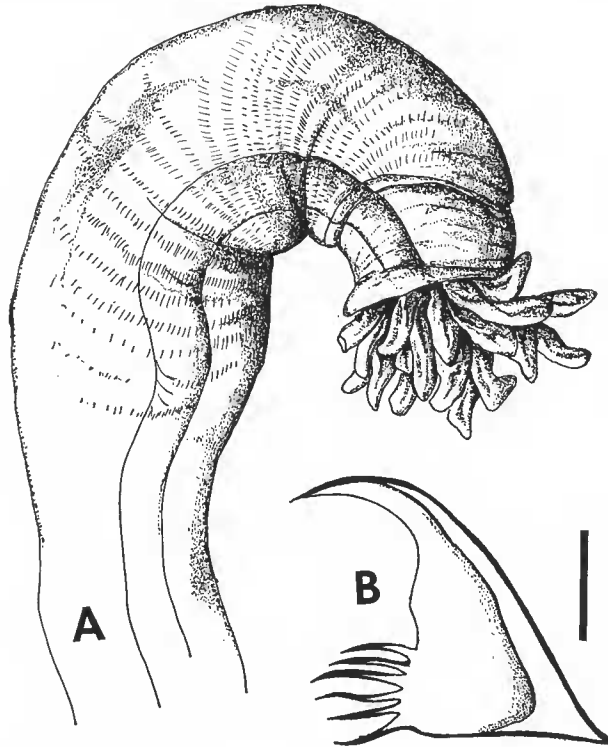


FIG. 4. — *Golfinzia pectinatoida* n. sp. : A, tentacles and tip of introvert ; B, introvert hook (scale = 10 μ m).

The trunk and most of the introvert are uniformly covered with large, low, oval, blister-like papillae. The size of these are directly related to the size of the animal. Their density is low enough so that the borders are not in contact with their nearest neighbors. The epidermis of many animals is rugose and loose appearing, often with wavy, zig-zag lines reminiscent of *G. catharinae* (fig. 3). The overall color ranges from white through tan to pinkish tan, most being a very pale tan. The length of the trunk ranges from 4-

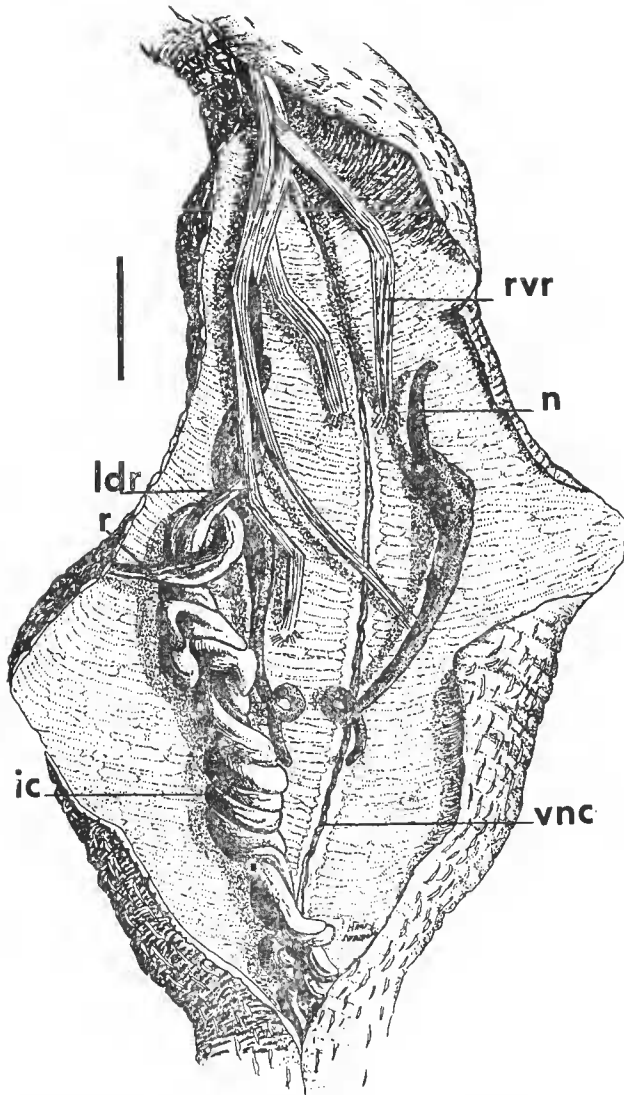


FIG. 5. — *Golfsingia pectinatoida* n. sp. Internal view.
ic = intestinal coil; ldr = left dorsal retractor; n = nephridium; r = rectum;
rvr = right ventral retractor; vnc = ventral nerve cord.

21 mm in this population. The diameter is usually 2-3 mm while the introvert is usually 1.5-2 times the length of the trunk. Normal *Golfingia* tentacles are present. In one worm with a 15 mm trunk and 25 mm introvert, there are 24-28 short tentacles present (fig. 4A).

Colorless hooks, measuring 25-30 μm in height are arranged in several rows (30 rows in the above worm) becoming scattered posteriorly. They are sharply bent with 4-6 (most have 5) spinelets at the base (fig. 4B).

Internally, the four slender retractor muscles originate in the first quarter of the trunk with the ventral pair anterior to the dorsal (fig. 5) in an atypical fashion. The use of dorsal and ventral here is perhaps misleading as both pairs originate quite close to the ventral nerve cord and the actual difference between the two is slight. The long, free nephridia have a short secondary lobe anterior to the nephridiopore which itself may be located near the level of the ventral retractor muscle origins or anterior to this point. The anus is posterior to the nephridiopore in the region of the retractor origins. The intestine is not anchored by a spindle muscle or fixing muscles. While most of these were free living in the sediment, a few were inhabiting empty gastropod shells.

The other members of this subgenus which have hooks, normal tentacles, no *Aspidosiphon*-like shields, and a rugose wrinkled epidermis are *G. mutabile* and *G. rugosa*. The nature of the retractor origins, nephridia, papillae, and hooks with spinelets easily distinguish this species from those two. The similarity of this species to those in the subgenera *Mitosiphon* and *Fisherana* (spinelets on hooks and bilobed nephridia) is interesting. The absence of a posteriorly attached spindle muscle in this species clearly separates these groups. Whether or not that particular character deserves such heavy weighting may be debatable. Perhaps this set of characters (bilobed nephridia, four thin retractor muscles, and spinelets on hooks) that we see in this form and in others such as *G. misakiana/hespera*, *G. murinae*, and *Phascolosoma pectinata* is simply an example of convergent evolution. It would be interesting to know if there was any adaptive value to spinelets on the hooks.

Except for the tentacles and longitudinal musculature, this species is strikingly similar to *P. pectinata*, hence its name.

The type specimen has been deposited in Muséum national d'Histoire naturelle, Paris. Holotype : Cat. n° AH-409 ; BT Station 801 ; "Grand Récif", Tuléar, Madagascar. Paratype : Cat. n° AH-410 ; BT Station 757 ; "Grand Récif", Tuléar, Madagascar.

***Golfingia* (*Golfingiella*) *pudica* (Selenka, 1885)**

HOE Sta. 371E ; 6 spec. ; 8/19/64 ; 24°46' S, 35°20' E ; 132 m ; Mozambique Channel.

These representatives of this uncommon and ill defined species are all small (2-12 mm trunks) and not in particularly good condition. As these specimens have the spindle muscle attached posteriorly, we are in agreement with WESENBERG-LUND (1959b) and place them in this subgenus (see CUTLER & MURINA, 1977).

The skin is loose fitting, thin, and pale brown/grey. In some it is wrinkled and exhibits transverse grooves. Numerous flat, pale papillae cover the surface. The introvert is a little longer than the trunk and bears rows of thin, pale, unidentate hooks 25-30 μm

high. Some of these hooks exhibit 3-4 basal plates at the anterior margin that appear occasionally like the start of spinelets.

The four thin retractor muscles have the normal arrangement, the ventral pair originating near the middle of the trunk and the dorsal pair originating more anteriorly, about half way between the ventrals and the nephridia. The short, single-lobed nephridia open at the same level as the anus and hang free in the coelomic cavity. A pair of eyespots is present.

The original description of this species by SELENKA is woefully brief and inadequate. He compared it to *G. vulgaris* but did not provide a real description nor any helpful figures (see STEPHEN & EDMONDS, 1972 : 104). Also, it is very similar to *Golfingia* (*Fisherana*) *capitata* and without an accurate grasp of the tentacular arrangement a *G. capitata* would key out to *G. pudica*. It might also be noted that this species co-occurs here along with *Aspidosiphon zinni* (the only record for this species from this region). *A. zinni* co-occurs with *G. capitata* off eastern United States. Therefore, these specimens are assigned to this taxon with reservations.

DISTRIBUTION. — The three previous records are from fairly cool, sublittoral water off Antarctica, Kerguelan Island, and Mauritius, so this is an additional record of an apparently southern ocean form.

***Golfingia* (*Mitosiphon*) *misakiana* (Ikeda, 1904)**

HOE Sta. JR 38-1 : 1 spec. ; 1/20/64 ; 13°24' S, 48°18' E ; 1 m ; Nosy Bé. — Sta. RU 242 : 3 spec. ; 11/14/64 ; 04°05' S, 39°40' E ; 1 m ; Mombassa.
Nosy Bé RP Sta. : 4, 8 spec. — BT Sta. : 556, 1 spec. ; 557, 2. *Enhalus acoroides* seagrass beds. Tuléar BT Sta. : Many, mainly in the medium and coarse sands on the reefs and lagoonal bottoms. Moorea BT Sta. : 27, 12 spec. ; 29, 11 ; 33, 4.

These 535 specimens make this troublesome species the most common form in these collections. The *Golfingia trichocephala/misakiana/hespera* complex is one of the less clear corners of sipunculian systematics at this point. They have been discussed by a few authors (e.g. CUTLER, 1973 ; AMOR, 1975) and more will be soon forthcoming. The basic distinction has been that *G. trichocephala* lacks hooks while the other two have hooks. The alleged differences between *G. misakiana* and *G. hespera* are thought to be papillae and/or number of accessory spinelets on the base of the hook. We found that most hooks in these specimens had from 4-6 spinelets. A review of this controversy will appear in CUTLER (1979). This subgenus has been redefined because of the recent discovery that at least two species have the tentacles dorsal to the mouth (fig. 6).

It is very difficult to determine the presence of hooks if the introvert is not everted sufficiently as the introvert is more than eight times the trunk length and very thin (less than 0.4 mm). Also the area that bears the 25-35 rows of hooks is very short (only the distal 2-4 %), and as the hooks are very small (15-25 μ m) and transparent. There are in this collection a few which have hooks showing but most do not. If the distal end of the introvert has been torn in the collecting process, no hooks will be found.

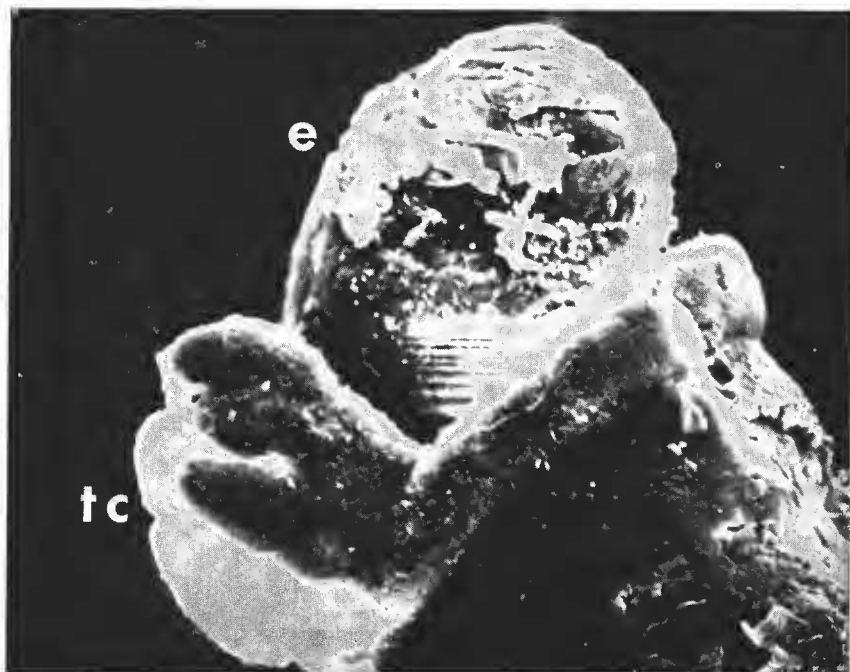


FIG. 6. — *Golfingia misakiana*. Esophagus (e) protruding through mouth ventral to tentacular crown (tc). (Scanning electron micrograph 200 \times .)

After prolonged consideration, we have decided to name these *G. misakiana*. The opacity and color of the body wall varies with the size as does the nature of the posterior papillae. All of these have some round papillae on the trunk, concentrated at the posterior end. It is still our opinion that FISCHER's *G. hespera* represent the larger, older part of this population with more opaque skin, larger papillae, and a larger number of spinelets on the hook and is, therefore, a junior synonym. A parallel situation is discussed in BERTSCH (1976) with respect to radular teeth in opisthobranch gastropods and how older taxonomic groups turn out to be little more than size categories which are later synonymized as researchers collect intermediate forms.

DISTRIBUTION. — There are published records of this species from Japan, California, Peru, Brazil and Western Australia. These new records from Madagascar, Mombassa, and French Polynesia suggest a circumtropical pattern.

***Golfingia* (*Mitosiphon*) *trichocephala* (Sluiter, 1902)**

IIOE Sta. 210B; 75 spec.; 11/16/63; 21°08' N, 69°48' E; 35 m; Arabian Sea. — Sta. 391F; 1 spec. (poor condition); 9/9/64; 29°26' S, 31°46' E; 77 m; Durban.
Nosy Bé RP Sta. : 3, 2 spec.; 5, 7; 8, 1; 9, 4; 11, 22; 13, 4.
Tuléar BT Sta. : Many, mainly in the medium and fine sands on the reefs, the lagoonal bottoms and also the littoral tidal flats with seagrass beds.

When SLUTER first described this species he overlooked some important features (bilobed nephridia and four retractors), so that upon re-examination of the type material a redescription was called for (CUTLER, 1967; 1973). At that time *G. tenuissima* and *G. longirostris* (WESENBERG-LUND, 1959b) were considered to be junior synonyms of this species. A lengthy discussion of the complex of related species (including *G. hespera* and *G. misakiana*) was presented.

When we began working with this collection, it was thought they were all *G. trichocephala* but when we found hooks on some, doubt began to enter and we thought we should consider them all *G. misakiana*. After lengthy consideration of much data it was decided to recognize two species: *G. misakiana* (with hooks, tentacles, and spheroid papillae on the posterior end of the trunk) and *G. trichocephala* (lacking hooks, tentacles, and trunk papillae). The internal anatomy, general form, and size are practically identical. They are generally 3-8 mm long with introverts 8-10 times the trunk length (CUTLER, 1973, has a complete description).

We believe we have seen the distal tip of the introvert and find only small papillae. There is still the possibility that none was completely extended so tentacles could be overlooked, but we are unable to demonstrate any. The very long, thin nature of the introvert makes it susceptible to damage and the torn end is deceptive.

It is difficult to envision how these two forms coexist so closely together. We thought perhaps an examination of gut contents would demonstrate a different food preference (different niche parameter) as one has tentacles and hooks, but this was not productive. We analyzed their sipunculan neighbors in the Tuléar area — with which other species do they live — but again can see no significant differences. *G. trichocephala* seems to be found by itself more often (22 versus 10 stations) and does not co-occur with quite as many other species (10 versus 14). They were found living at the same station 11 times (out of 87). They both occur most often with *Siphonosoma cumanense* and *Aspidosiphon thomassini* (this latter is remarkably similar in size and shape).

Whether or not earlier authors had "pure" collections or a mixture of these two species is uncertain. If the introvert is not completely out and one does not look very closely for the papillae, some *G. misakiana* could easily be overlooked and called *G. trichocephala*. It is also possible that *G. tenuissima* is *G. misakiana* in which hooks were not seen (compare figures of papillae in WESENBERG-LUND, 1959b, and AMOR, 1975).

DISTRIBUTION. — Previous reports from off Indonesia, South and West Africa, and southeastern United States all from shallow, warm water are now supplemented by these from Madagascar and the Arabian Sea. Unpublished records from the Gulf of Mexico, Australia, Coral and Tasman Seas, and Singapore suggest a circumtropical species.

***Golfingia (Phascoloides) minuta* (Keferstein, 1853)**

HOE Sta. 390S; 59 spec.; 9/9/64; 29°35' S, 31°42' E; 138 m; Durban.

The trunk length in this collection measures 1.5 to 12 mm and all are 1 mm or less in diameter. The largest worm has scattered hooks measuring 25-32 μ m high.

DISTRIBUTION. — This common Atlantic Ocean species has been often recorded from cold waters in both north (up to 70° N) and, less often, south Atlantic. It also occurs in the Mediterranean, two records from the northwest Pacific, and one from Chile. One earlier record, also from the Durban area, is the only other Indian Ocean record. It is interesting to speculate about its dispersal into the Pacific via a northern Arctic and southern route, and into the Indian Ocean via a southerly route.

Golfingia (Phascoloides) rutilofusca (Fischer, 1916)

Golfingia sp. Stephen & Cutler, 1965 : 115.

IIOE Sta. 221A ; 1 spec. ; 11/18/63 ; 22°32' N, 68°06' E ; 58 m ; Arabian Sea, NW Bombay. — 230B ; 1 spec. ; 11/20/63 ; 23°31' N, 66°55' E ; 88 m ; Arabian Sea. — 391F ; 7 spec. ; 9/9/64 ; 29°26' S, 31°46' E ; 77 m ; Durban. — 39111 ; 1 spec. ; 9/9/64 ; 29°21' S, 31°35' E ; 57 m ; Durban. — 392K ; 7 spec. ; 9/10/64 ; 29°19' S, 31°36' E ; 38 m ; off Durban OR 391C 9/9/64 ; 29°29' S, 31° 45' E ; 86 m ; (label confusion at SOSC). — 408A ; 1 spec. ; 10/15/64 ; 16°43' S, 43°43' E ; 60 m ; NW Majunga, Madagascar. — 409 I ; 1 spec. ; 10/19/64 ; 16°03' S, 44°09' E ; 25 m ; NW Majunga, Madagascar.

Nosy Bé RP Sta. : 1, 2 spec.

Tuléar BT Sta. : D10, 1 spec. ; D13, 1 ; D29, 1 ; D57, 3 ; 193, 1 ; 620, 3 ; 621, 3 ; 622, 14 ; 633, 2 ; 728, 2 ; 766, 1 ; 774, 2 ; 779, 6 ; 810, 2 ; 813, 1. Frequent in sediments (medium sands to clay) of lagoon or enclosed lagoon bottoms.

This sample of 66 worms varying in trunk length from 2-15 mm is especially important for three reasons : the information it gives us about the variable nature of the posterior end of the trunk, the first view of its unique tentacular arrangement, and the resolution of the issue of the spindle muscle raised in the literature (see STEPHEN & EDMONDS, 1972:155).

FISCHER's original description of this form was based on « many » specimens from 1362 m off Zanzibar. He placed it in the genus *Aspidosiphon* because of the shield like nature of the posterior end which he figured (FISCHER, 1922) as very coarsely grooved with a definite apex. This is now clearly seen to be dependent on the state of contraction/relaxation of the body wall at the time of fixation. A wide range of conditions is found from smooth and rounded to grooved and pointed (fig. 7a and 7b). The majority are more rounded than pointed. FISCHER obviously had very strongly contracted worms.

FISCHER's comments on the number of tentacles and length of introvert suggest to us he had no specimen with completely extended introverts. In this collection the introverts are five to six times the trunk length and several show approximately 30 unique tentacles (fig. 8a and 8b). They are slender, unbranched and come from a pad-like zone along the dorsal side of the tip of the introvert, somewhat like the « fingerprint » portion of a finger. The mouth is at the distal tip with a few tentacles around it. This arrangement is unlike any other known sipunculans. Hooks are absent.

The coloration is not always a uniform red but sometimes has a blotched appearance, especially in the larger animals patches of yellowish-white are present (fig. 9). Also, the distal half of the introvert gradually loses all pigmentation. It is still a very striking worm.

Internally, the two retractor muscles attach in the last fifth of the trunk and the free nephridia open anterior to the anus. The gut is not formed into a tight, regular coil as

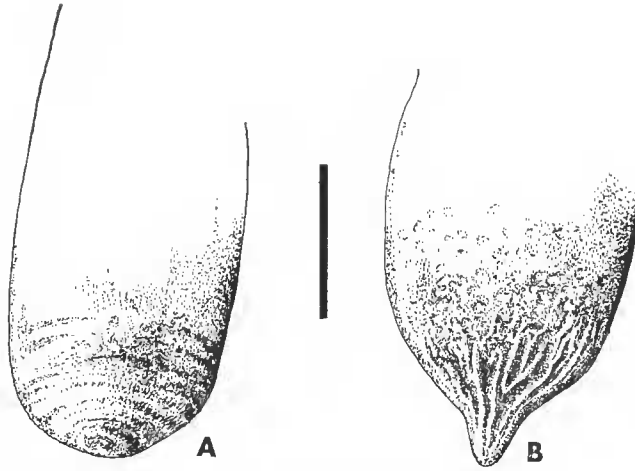


FIG. 7. — *Golfinigia rutilofusca* : A, relaxed, rounded posterior end of trunk ;
B, contracted, pointed posterior end of trunk. (Scale 2 mm.)

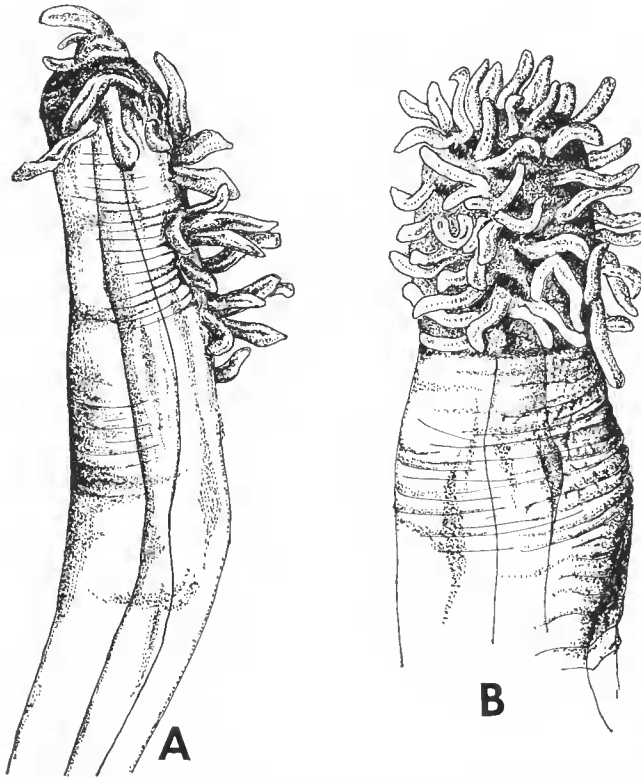


FIG. 8. — *Golfinigia rutilofusca*. Tentacular region : A, side view ; B, dorsal view.

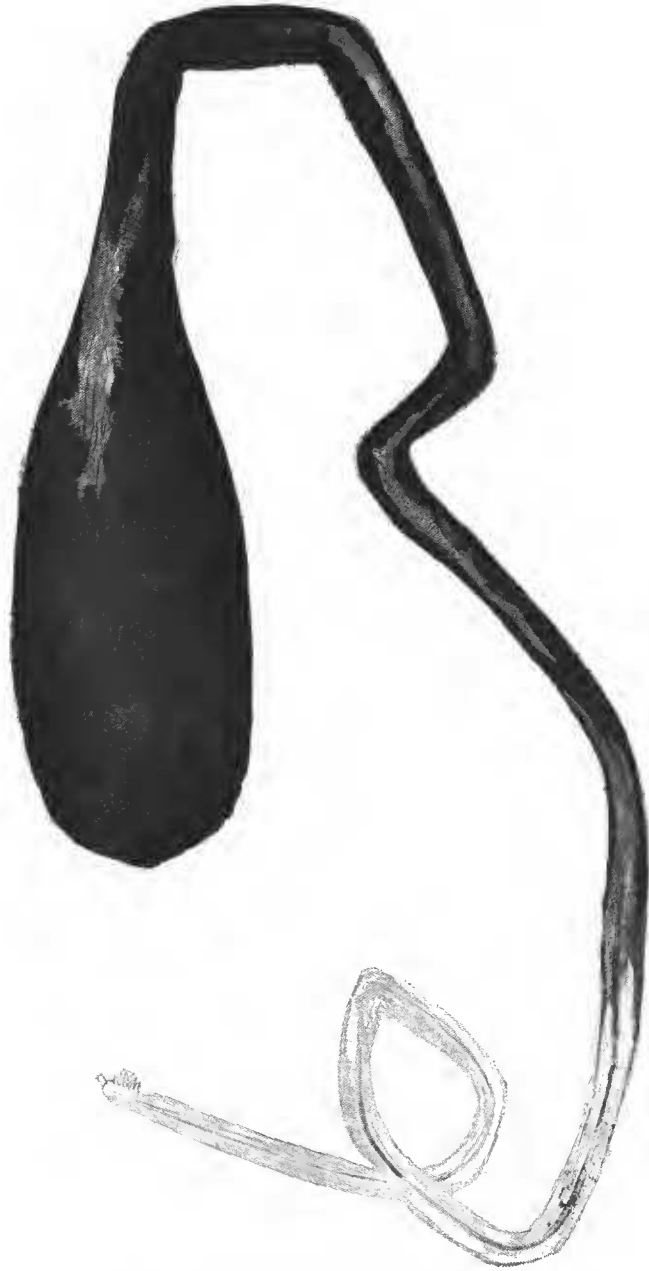


FIG. 9. — *Golfinia rutilofusca*. Whole worm.

in most *Golfingia* but is loosely coiled and the whole mass is free to move. The oesophagus remains attached to the retractors for a considerable distance so when the introvert is extended, the front end of the coil is near the anterior end of the trunk. However, when the retractor museles are contracted, this region of the gut coil is pulled back to almost the posterior end of the trunk. No evidence of a spindle musele is present. A well defined wing musele anchors the anal region of the rectum to the body wall.

DISTRIBUTION. — The three earlier records of this species come from Durban, Mozambique, and Zanzibar at depths from 57-1562 m. This is the first from Madagascar or India and the first from such shallow water.

Golfingia (Phascoloides) sp.

IIOE Sta. JR 38-10; 6 spec.; 1/20/64; 13°24' S, 48°18' E; 1 m; Nosy Bé, stones and mud. — JR 33-15; 3 spec.; 1/15/64; 13°26' S, 48°23' E; 1 m; Nosy Bé, under intertidal rocks.

Tuléar BT Sta. : 843B, 1 spec.

All of these specimens are less than 5 mm long and probably juvenile forms of some member of this subgenus. It is tempting to assign a name to them, but they are simply too nondiscript for us to do so. They are similar to both *G. minuta* and *G. pellucida* in many ways.

Phascolion beklemischevi Murina, 1964

IIOE Sta. 371F; 2 spec.; 8/18/64; 24°46' S, 35°18' E; 110 m; off southern Mozambique.

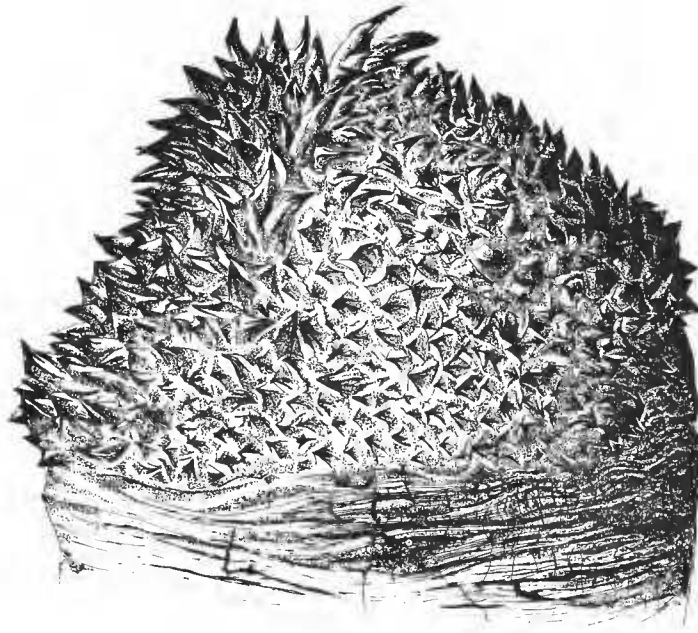
These are small, transparent worms lacking holdfasts but bearing round, flat papillae. The sharp hooks are strongly bent and in the smallest one (trunk plus introvert measures 2 mm), the trunk was about twice the length of the introvert. The larger one (5 mm) had been taken from a gastropod shell. The two retractor museles originate from very near the posterior end.

DISTRIBUTION. — The only other record of this form is the original description from the southern Mediterranean Sea so this is a significant extension of its known range.

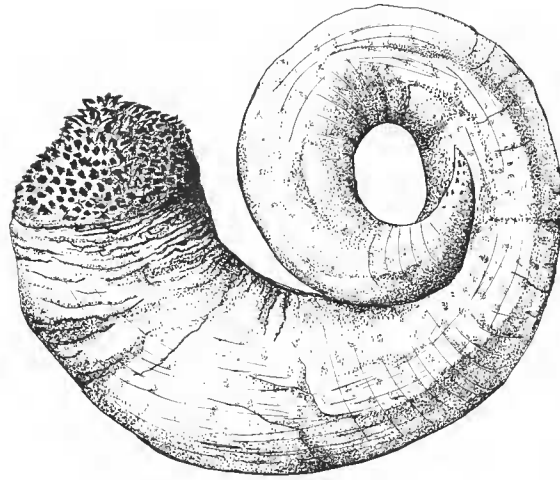
Phascolion megaethi n. sp.

Tuléar BT Sta. : 64, 2 spec.; 788, 1; 790, 1; 801, 2; 803, 2. More frequently in the sediments clogging the outer boulder tract; accidently in a sand dune of the reef inner slope in the lagoon.

These eight worms from five stations range in size from 4-12 mm. Most are from gastropod shells. The trunk is pale and smooth with large, dark red-brown, mammiform papillae (100-150 μ m in height) around the anterior end of the trunk which at first



B



A

FIG. 10. — *Phascolion megaethi* n. sp. : A, external view (scale = 1 mm) ; B, anterior end of trunk.

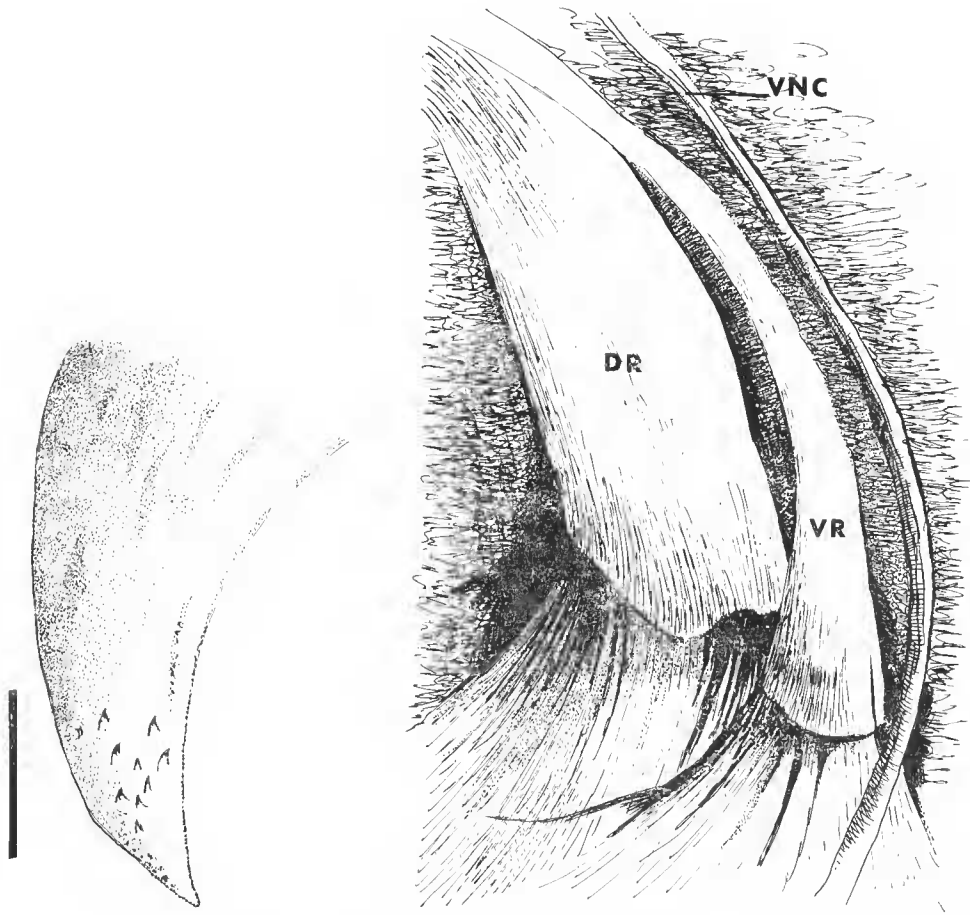


FIG. 11-12. — *Phascolion megaethi* n. sp. : 11, holdfasts on posterior tip of trunk (scale = 0.5 mm) ; 12, retractor origins near posterior tip. DR = dorsal retractor; VNC = ventral nerve cord; VR = ventral retractor.

glance resembles an *Aspidosiphon* shield (fig. 10). Holdfasts are few and small, single pointed, triangular structures restricted to the posterior end of the trunk (fig. 11). On one large specimen they are arranged in two rows around the narrowed posterior tip, in others they are scattered. The introvert bears few, scattered, short, blunt hooks (30-35 μ m in height). There are fewer than 15 tentacles present.

Internally the two retractor muscles originate near one another, each from a single root, but in an unusual fashion. The ventral muscle is about one half the diameter of the dorsal and originates slightly behind the dorsal (fig. 12). The intestine has the normal, loose *Phascolion* loops and no apparent coils.

There are several species in this genus with two retractors, adhesive papillae and hooks.

P. heteropapillosum is similar externally but the fewer number of tentacles, darker papillae at the anterior end of the trunk, the holdfasts with a single tooth, and the nature of retractor muscle origins sets this species apart. The name refers to the large red-brown nature of the papillae around the anterior end of the trunk.

The type material has been deposited in the Muséum national d'Histoire naturelle, Paris. Holotype : Cat. n° AH-412 ; BT Sta. 788 ; "Grand Récif", Tuléar. Paratype : Cat. n° AH-413 ; BT Sta. 790 ; "Grand Récif", Tuléar.

Phascolion pharetratum Sluiter, 1902

Tuléar BT Sta. : 228, 1 spec. ; 240, 3 ; 654B, 1 ; 741, 1 ; 843, 2. In coarse sediments of the reef front.

These animals were taken from gastropod shells and belong to this uncommon species on the basis of their peculiar, numerous, large, bent, dull, dark brown hooks and absence of holdfasts. At the base of the introvert of one specimen is a thick colony of entoprocts. There are also colorless mammiform papillae around the introvert base and filamentous tentacles are visible on the worm from Sta. 228. The midtrunk region is smooth and almost transparent. The two retractor muscles of unequal size originate well in front of the posterior end.

DISTRIBUTION. — These records are the first since its original description from the other side of this ocean off Malaya.

Phascolion strombi africanum (Fischer, 1923)

Phascolion africanum Fischer, 1923 : 5 ; WESENBERG-LUND, 1963 : 134-135.

Tuléar BT Sta. : A1, 1 spec. ; 62, 2 ; 63, 4 ; 91, 1 ; 630, 1 ; 737, 1 ; 889, 1 ; 906, 1. In medium and fine sands of sand banks on reef or of the lagoon (inner reef slope, lagoonal bottoms).

Phascolion africanum (Fischer, 1923) was described from a single specimen. The only other report was WESENBERG-LUND (1963) from three damaged specimens. These 12 animals give evidence which strongly suggests the wisdom of reducing this taxon to subspecies rank as the differences from *P. strombi* are very slight. It seems logical to consider this a geographically isolated population which has deviated somewhat from the main stock.

The distinction made in STEPHEN & EDMONDS (1972) centers on *P. strombi*'s holdfasts having one or more teeth while *P. africanum* supposedly lacks these points on the holdfasts. While it is true that most are semicircular or U-shaped, a few do have distinct points or teeth on them. The smallest animals (about 2-3 mm) have papillae which have not yet developed the chitinized rims or borders. It seems evident from other collections also, that the nature of these papillae varies according to age and microhabitat. HYLLEBERG-KIRSTENSEN (1975) has also suggested that they may not be, in fact, attachment papillae (holdfasts) but rather serve an internal housekeeping/cleaning function.

The hooks measure 50-70 μm high and there are about 40 tentacles on the larger worms. The two retractor museles originate near the posterior end, the thinner ventral one being a little behind the larger dorsal musele. In the one from Sta. 889, there is a tendency for the longitudinal museles to divide into separate bands at the anterior end of the trunk as is sometimes noted in larger *Aspidosiphon* (*Aspidosiphon*).

DISTRIBUTION. — The previous records of this form come from off Cape Province, South Africa, so this constitutes a slight extension of its range.

***Phascolion valdivae* Fischer, 1916**

HOE Sta. 390S; 13 spec.; 9/9/64; 29°35' S, 31°42' E; 138 m; off Durban.

These worms, whose size range is 7-25 mm, fit FISCHER's description fairly well. The tall, slender, spikelike hooks measure 80-95 μm . There are two introverts in the sample, unattached to any trunk, which looked similar but the hooks on these were only 50-70 μm high. They may have come from smaller worms. These animals were thin-walled, semi-transparent, and came from seaphopod shells. One had a commensal polychaete with it.

The intestine is not loosely looped as in many *Phascolion* but is in a well defined coil. The holdfasts do not have a pigmented chitinous rim but are circular/oval and flat, some having a clear, thickened border. The nephridium is short and attached for most of its length, not free as FISCHER notes. The single retractor musele has a broad origin which is bifurcated.

DISTRIBUTION. — The sole other report of this species comes from St. Paul's Island from a seaphopod shell at 158 m, so this species seems to be a southern Indian Ocean form so far.

***Phascolion* n. sp.**

HOE Sta. JR-2; 1 specimen from gastropod shell; 12/28/63; 13°26' N, 48°23' E; 1 m; Nosy Bé, Madagascar.

This single specimen has a trunk measuring about 15 \times 5 mm and the introvert is completely retracted. The epidermis is semi-transparent and colorless except for the anterior quarter where it becomes thicker, more heavily papillated, opaque, and white. Large papillae are present and more concentrated anteriorly, but chitinized holdfasts (adhesive or attachment papillae) are lacking. Also lacking are introvert hooks, but normal tentacles are present.

Internally the gut is thrown into loops but no coils, fixing museles hold this in place. The nephridium is about 1/3 the trunk length, fragile, and partially attached, opening posterior to the anus. The dorsal retractor musele originates at the left side of the ventral nerve cord anterior to its termination, and from three roots. The ventral is 1/5 to 1/6 the size of the dorsal and originates 2 mm posterior to the origin of the dorsal.

In this genus there are only three species (*P. botulum*, *P. artificiosum*, and *P. sandvichi*) with two retractors and hooks absent, but all of these have adhesive papillae which this form lacks, making it distinct. This is left unnamed in keeping with our philosophy that species are populations and it is necessary to have more than a single specimen to produce a meaningful new species description.

***Themiste lagenformis* Baird, 1868**

HOE Sta. JR 13-1; 16 spec.; 12/26/63; 13°24' S, 48°19' E; 1 m; Nosy Bé; in hard clay and rock.
Fort-Dauphin, DECARY coll., 1932, 2 spec.

Within this genus these 18 worms with two retractor muscles and short villi belong to Group 2 (STEPHEN & EDMONDS, 1972: 194). Having no hooks and short branching villi they are very similar to *T. robertsoni*. The main distinction seems to be the number of tentacular stems and whether there are four or six. However, when the introvert is retracted, this is very difficult to precisely ascertain. Also, the literature is not consistent and as STEPHEN & EDMONDS (1972: 205) point out: "The species is not always easy to identify". They then elaborate further on the problems. In RICE & STEPHEN (1970) where they redescribe *T. hennahi*, it is pointed out that three specialists looking at the same worm saw four, five, and six main stems. This identification is made with some reservation.

These specimens range in trunk length from 4-15 mm. The nephridia which are as long as the trunk open a little posterior to the anus. The two retractor muscles originate in the posterior fifth of the trunk.

DISTRIBUTION. — *Themiste lagenformis* (previously *T. signifer*) has been reported many times from the Indo-West Pacific area including Madagascar. Single records from Argentina and West Africa are the only ones from outside this area.

***Themiste lissa* (Fisher, 1952)**

HOE Sta. 357B; 2 spec.; 7/29/64; 29°11' S, 32°02' E; 68 m; Durban.

These two completely retracted tan specimens, 11 and 12 mm long, differ from the other herein reported members of this genus by having long, thin tubules coming off the contractile vessel. They have two retractor muscles, lack hooks, and three fixing muscles are present. The anus is anterior to the nephridiopores. In STEPHEN & EDMONDS (1972: 194) there are six species in Groups 3 and 4 that are very similar (see also RICE & STEPHEN, 1970: 36 where they come to a similar conclusion). Four of these were described by W. K. FISHER and five came from the California coast while the sixth is reported from Peru and Chile. *T. lissa* and *T. schmittii* are separated from the others because their nephridiopores are posterior to the anus, a character whose constancy is open to some question. For example, when RICE & STEPHEN (1970: 35) redescribed *T. hennahi*, one

of the other four, they said "nephridiopores open slightly posteriorly to the anus", not anterior as in STEPHEN & EDMONDS (1972). The alleged differences between these species are subtle, but we will not deal with that issue herein.

DISTRIBUTION. — This is the first report of this species since its original description from the intertidal zone of southern California, a rather striking extension of its range.

Themiste minor (Ikeda, 1904)

HOE Sta. 370H; 1 spec.; 8/18/64; 24°40' S, 35°28' E; 347 m; Mozambique Channel.

This single, small specimen (5 mm trunk) has a whitish trunk with brown pigment towards the anterior end where it is also hosting a colony of endoprocts. The introvert is withdrawn but hooks are present measuring 50-60 μ m in height.

Internally there are two retractor muscles, the nephridia open slightly anterior to the anus, and there are short, unbranched contractile vessel villi.

According to STEPHEN & EDMONDS' (1972: 194) scheme, this worm belongs to Group 2 and within this group is similar to *T. lagenformis* and *T. buttoni*. *T. lagenformis* is said to lack hooks and *T. buttoni* has branched contractile vessel villi. This latter distinction is troublesome as it would appear possible for a young *T. buttoni* to produce villi which begin as unbranched structures, only later, as they increase in size to bifurcate. This has been noted in *Golfingia catharinae* (Cutler, 1973). The small size of this worm makes it suspect, but this taxon seems most logical for now.

DISTRIBUTION. — Previous records of this species come from China, Japan, New Zealand, and the Tasman Sea then skip across the Indian Ocean to South and South West Africa. This specimen reinforces its presence in this corner of this ocean.

Themiste robertsoni (Stephen & Robertson, 1952)

HOE Sta. Te Vega 72 LH 4; 1 spec.; 10/19/63; 01°16' N, 103°48' E; 1 m; Singapore beach.
— India, N of Okan Point; 2 spec. 3/9/63; 22°30' N, 69°04' E; 1 m. — JR-24A; 1 spec.; 1/4/64; 13°24' S, 48°17' E; 1 m; Nosy Bé; mud flat. — JR 38-1; 9 spec.; 1/20/64; 13°24' S, 48°18' E; 1 m; Nosy Bé; rock and coral.

Tuléar, coll. LEGENDRE, 1964, 8 spec.

These 21 worms ranging in size from 4-30 mm are also in STEPHEN & EDMONDS' Group 2 (1972: 194). The absence of hooks, the blue area towards the introvert tip, and tentacular arrangement help place them in this taxon which is very similar to *T. lagenformis*. The introvert is less than half the trunk length and numerous short villi can be seen. The anus and nephridiopores are at nearly the same level. This group does look different than those we've called *T. lagenformis*, but sometimes the decisions are uncomfortably subjective. It is hoped that some revisionary work in this genus will be forthcoming soon.

DISTRIBUTION. — This species has been known from only Zanzibar and South Africa, so these records from Madagascar, India, and Singapore are a major northerly and easterly extension of its known range making it a member of the Indo-West Pacific shallow water fauna.

***Aspidosiphon (Aspidosiphon) zinni* Cutler, 1967**

IIOE Sta. 371E ; 5 spec. ; 8/19/64 ; 24°46' S, 35°20' E ; 132 m ; Mozambique Channel.

All of these small (3-5 mm), slender and transparent worms had their introverts withdrawn but small, scattered, single-pointed hooks could be found and in other ways they match this species. Their general shape and size is similar to *Golfingia minuta* but the " flat " anterior end with its granular anal shield is distinctive.

DISTRIBUTION. — The only other published records of this species are on the continental slope and rise off the Atlantic coast of the United States and Bermuda between 1 100-3 000 m. There are unpublished records from elsewhere in the Atlantic Ocean (north and south) but these are the first record for the Indian Ocean.

***Aspidosiphon (Aspidosiphon) elegans* (Chamisso & Eysenhardt, 1821)**

IIOE Sta. HA 39 ; 2 spec. ; 1/12/64 ; 27°16' N, 33°47' E ; 2 m ; Red Sea. — HA 67-40 ; 3 spec. ; 7/10/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia. — B-3 ; 1 spec. ; 2/9/63 ; 12°00' S, 96°50' E ; 1 m ; Cocos-Keeling Islands, reef.
New Hebrides, Sta. 988 ; 9 spec. coll. DE GAILLANDE.

These fifteen specimens were easily referable to this species, with their large spines covering most of the introvert proximal to the hooked region. These dark brown spines show considerable variation in number, size, and density along the introvert which showed an interesting correlation with hook sharpness. Those specimens with sharply pointed hooks have a dense population of spines whereas when fewer spines are present, the hooks have a duller apex. In addition, on any single worm, the larger spines were found on the dorsal side of the introvert and these were also more sharply bent towards the posterior end of the organism. Those on the ventral side tend to be smaller and less bent. It was also observed that the smaller the spine, the straighter it was. In the rest of their morphology, these specimens nicely match the description given in STEPHEN & EDMONDS (1972 : 235). The trunk length ranges from 10-58 mm. The size of the dark platelets on the anal shield is quite variable.

DISTRIBUTION. — This species has been found from the Red Sea down the coast of East Africa to Mozambique and Mauritius. It then occurs in Malaya, Japan, and several West Pacific Islands. A single report from Florida of a single, desiccated specimen (WESERBERG-LUND, 1954) does not fit this apparently Indo-West Pacific shallow water form herein reported for the first time from the central and eastern Indian Ocean.

Aspidosiphon (Aspidosiphon) exhaustus Sluiter, 1912

IIOE Sta. 206A; 2 spec.; 11/15/63; 20°21' N, 69°58' E; 75 m; Arabian Sea, NW Bombay. — 358A; 5 spec.; 7/30/64; 29°19' S, 32°00' E; 366 m; Durban. — 370H; 3 spec.; 8/18/64; 24°40' S, 35°28' E; 347 m; Mozambique Channel. — 390E; 2 spec.; 9/8/64; 29°42' S, 31°38' E; 350 m; Durban. — 408D; 1 spec.; 10/15/64; 16°42' S, 43°19' E; 225 m; NW of Majunga, Madagascar.
Tuléar BT Sta. 62, 4 spec.

These 17 specimens with single pointed hooks (varying in size from 13 μ m in a 2 mm worm to 35 μ m in a 28 mm worm), followed by a region of straight spines, are referable to this species. The anal shield is medium to dark brown, with well defined margins, short grooves dorsally and granular region ventrally. The caudal shield is less pigmented but usually well defined and bears about 20-25 radiating grooves.

The introvert is longer than the trunk. The nephridia open at the level of the anus, are attached from 50-100 % of their length, and the spindle muscle is attached posteriorly. The retractor muscle appears as a single muscle with two roots, or as two muscles which fuse. One worm from Sta. 206A has a retractor muscle which is a single muscle near its insertion at the head, then divides into two, but fuses into one again, then splits into two roots where it originates at the posterior end. GIBBS (1973) discussed a related case of splitting and fusing in detail for *Golfingia rimicola*. A rectal caecum is present.

Most of these came from scaphopod shells but those from Sta. 62 were living in gastropod shells. One from 206A has a small commensal bivalve mollusc attached by byssal threads to its posterior end. The three worms from Sta. 370H are less than 2 mm long but seem to fit into this group with some reservations. The Tuléar worms (Sta. 62) also differ from the rest (gastropod shells, shallow depth, anal shield differences) and may represent a subspecies or an ecological variety; it is also placed here with some reservations.

DISTRIBUTION. — These records are a valuable addition to a rather peculiar pattern. There are two reports from northwestern Africa (Congo and Morocco), one from south eastern Australia, one from the Gulf of Tonkin/ Indo-China, and one from Isle de Paoeua in the southern Pacific Ocean. These being the first from the western Indian Ocean suggests the possibility of a widespread deeper water (approximately 50-750 m) member of this genus which is absent from either side of the Americas.

Aspidosiphon (Aspidosiphon) jukesii Baird, 1873

IIOE Sta. JR 22-5; 4 spec.; 4/2/64; 13°24' S, 48°13' E; 1 m; Nosy Bé; volcanic rock. — JR 32-10; 2 spec.; 4/14/64; 13°34' S, 48°18' E; 1 m; Nosy Bé; mud/sand and rock. — JR 33-2; 1 spec.; 4/15/64; 13°26' S, 48°23' E; 1 m; Nosy Bé; dead coral. — JR 38-1; 11 spec.; 4/20/64; 13°24' S, 48°18' E; 1 m; Nosy Bé; rock and coral. — 270A; 1 spec.; 12/4/63; 22°07' N, 59°48' E; 56 m; Gulf of Oman. — 371F; 1 spec.; 8/18/64; 24°46' S, 35°18' E; 110 m; South Mozambique. — 372L; 11 spec.; 8/19/64; 25°07' S, 34°34' E; 112 m; South Mozambique. — 372M; 2 spec.; 8/19/64; 25°03' S, 34°31' E; 55 m; South Mozambique. — 372P; 5 spec.; 8/24/64; 25°57' S, 33°02' E; 37 m; South Mozambique. — 372Q; 2 spec.; 8/22/64; 25°57' S,

33°02' E; 42 m; South Mozambique. — 390S; 226 spec.; 9/9/64; 29°35' S, 31°42' E; 138 m; Durban.

Nosy Bé RP Sta. 6, 1 spec.

Tuléar BT Sta. : Many, free in gastropod shells or associated with free living corals (*Heteropsammia michelini*, *Heterocyathus aequicostatus*) alive or dead. In sediments from coarse sands to very fine sands generally.

Moorea BT Sta. 32, 1 spec.

Many of these 503 specimens had inhabited gastropod shells and solitary corals while alive and therefore, accurate measurements were impossible to obtain, but the largest worms are between 15 and 20 mm, very few over 10 mm, many around 5 mm, and a few about 1.5-2 mm. Their internal anatomy closely fit that presented in STEPHEN & EDMONDS (1972 : 228). Of particular interest is a statement they make which supports my argument for not using the condition of the longitudinal musculature as a generic character : " Longitudinal muscles continuous except anteriorly where they tend to split. "

On the same page they state : " ... carries about 40 rows of single-pointed hooks " and their key to this taxon is similarly constructed. However, in RICE & STEPHEN'S (1970) redescription of the type (wherein they submergered the better known junior synonym of *A. corallicola* Sluiter) they say the hook has a " secondary terminal point " as have other authors. CUTLER (1965) notes : " The secondary tooth on the hook is quite variable in size but usually present ". After examining many hooks from different sized worms, we propose the following : A secondary point on the hook is analogous to a grey hair. It usually develops only in mature individuals and at different ages (some prematurely, others very late), but it is not present in young forms. The timing and degree of expression is variable but age (size) related and not uniformly present within a large population made up of different ages and races.

A second set of observations, on the nature of the anal shield, led to the following conclusions : The appearance of this structure changes with age also. We have identified three " stages " in this sequence. Stage 1 — distinct longitudinal grooves dorsally and a ventral area of spine-like processes. Stage 2 — the longitudinal grooves become more restricted to the dorsal margin, there is a central region of irregular rectangles with occasional suggestions of transverse ridges and grooves, and a narrow ventral zone of spines. Stage 3 — only remnants of grooves on the dorsal edge, a narrow strip of spines ventrally, and most of the surface covered with granules or rectangles. These are generalizations, but as such hold true most of the time. The idea that these are fixed and unchanging structures is fallacious.

DISTRIBUTION. — These records, together with earlier ones from Madagascar, Zanzibar, Gulf of Manaar, Ceylon, and Malaya support its membership in the Indian Ocean shallow water fauna. It is the second most common species in these collections.

Aspidosiphon (Aspidosiphon) kovaleskii Murina, 1964

IIOE Sta. 391J; 3 spec.; 9/9/64; 29°21' S, 31°35' E; 57 m; Durban. — 392K; 4 spec.; 9/10/64; 29°19' S, 31°26' E; 38 m; Durban. — 394B; 1 spec.; 9/25/64; 29°27' S, 31°31' E; 70 m; Durban. — 453; 5 spec.; 12/17/64; 11°11' N, 51°14' E; 48 m; Somalia-Gulf of Aden.

These 13 specimens range in size from 3-18 mm. The introvert carries scattered, single-pointed hooks about 20-25 μ m tall. The anal shield is grooved and has spines along the ventral margin. However, in the smaller (3-4 mm) specimens this same area has granular units which evidently continue to grow and become spine-like structures. The borders are quite distinct. Internally the gut is attached posteriorly by a spindle muscle. The two roots of the retractor muscle have their origins from the posterior end of the trunk and the nephridiopores open at the same level as the anus. At least one of the specimens was inhabiting an empty scaphopod shell as were the holotypes.

DISTRIBUTION. — Previous records of this species are from the Aegean, Adriatic and Red Seas and the Gulf of Aden. These specimens from the western edge of the Indian Ocean are a major southerly expansion of this range.

Aspidosiphon (Aspidosiphon) venabulus Selenka, de Man & Bulow, 1883

Tuléar BT Sta. : D1, 2 spec. ; D2, 2 ; D9, 4 ; 365, 4 ; 606, 1 ; 652, 1 ; 813, 3. In very fine sands and silts, more frequently in lagoonal bottoms.

These 17 specimens lacking hooks, with a single retractor muscle, and a dark anal shield are easily referable to this species. The anal shield is granular in some and coarser in others with reduced spines or large, pointed, wart-like units on the edge and with a grooved appearance in most. The nephridia are about as long as the trunk, attached for 2/3 their length, and open posterior to the anus. A single fixing muscle is present and the spindle muscle is attached posteriorly. The two roots of the retractor muscle originate at the posterior end of the trunk. These specimens are between 5 and 15 mm long, some from gastropods and others were not coiled, having inhabited some other shelter.

DISTRIBUTION. — All five of the previous records of this species are from West African waters. These Madagascar worms are then the first record from the Indian Ocean.

Aspidosiphon (Aspidosiphon) thomassini n. sp.

HOE Sta. HA 67-40 ; 1 spec. ; 7/10/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia.

Nosy Bé BT Sta. : 553, 1 spec. ; 554, 1 ; 556, 1. *Enhalus acoroides* seagrass beds.

Tuléar BT Sta. : 196 specimens collected in 53 stations, most frequently in the medium sands and fine sands with no more 10 % of silt, and more commonly on the bottom of the reef pools, in the seagrass beds and the bottoms of enclosed lagoons and of the lagoon, in the reef area, but also in the terrigenous littoral seagrass beds.

Moorea BT Sta. : 19, 6 spec. ; 27, 20 ; 29, 13.

One of the more distinguishing characteristics of this species is that the introvert is not at the typical 90 degree angle from the trunk but rather comes off at less than 60 degrees, usually at 40-45 degrees, from the main axis of the trunk. This introvert is from 2-4 times the trunk length. The trunk length varies in this population from 1.5-7 mm

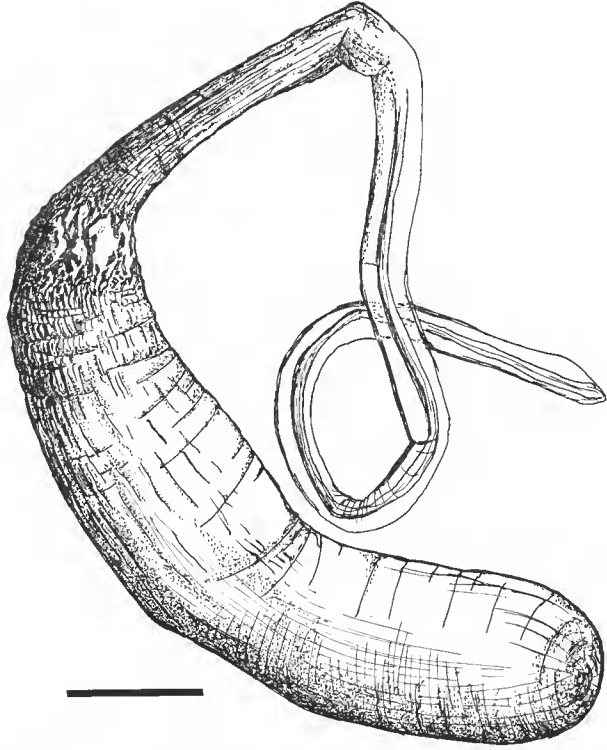


FIG. 13. — *Aspidosiphon thomassini* n. sp. Whole animal. (Scale = 1 mm.)

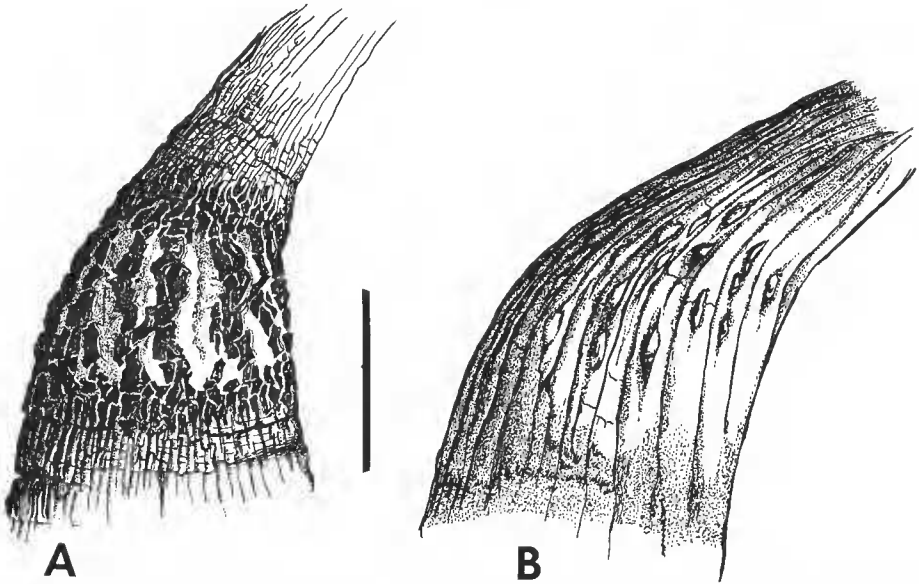


FIG. 14. — *Aspidosiphon thomassini* n. sp. Anal shield : A, well defined ; B, poorly defined. (Scale = 1 mm.)

and in diameter from a little less than 1 mm to 3 mm while the introvert diameter measures 0.5-1 mm (fig. 13). The color of the preserved material ranges from a reddish brown to an off-white, most being a light reddish tan. No worms in this collection have their introverts completely extended so the nature of the tentacles cannot be commented on. Hooks were not observed.

The anal shield is often poorly defined and quite variable (fig. 13, 14). In those where it is well developed, the chitinous plates are randomly placed and low in profile, sometimes gathered into longitudinal and possibly in transverse rows forming low ridges with intervening furrows. The average diameter of the platelets decreases towards the edge of the shield. The posterior dorsal margin is distinct often, but not outstanding. At the other end of the variation are shields made up of only a few scattered platelets disbursed in a rough, slightly grooved epidermis with no clear borders. Most animals exhibit something intermediate to these two extremes. The caudal end of the animal is essentially without a shield but may show a ringed appearance and be somewhat more rough or rugose. In a few larger individuals a vague suggestion of radiating grooves is apparent. No skin papillae are visible, but scattered flattened skin glands (as in *Siphonosoma*) may be present. The trunk surface is generally smooth, but under magnification often has a reticulate surface with faint annular and longitudinal grooves giving a vague *Sipunculus*-like appearance. This condition is more obvious in the darker colored individuals and may be due to a preservation technique.

Internally the single-lobed nephridia are attached for almost their entire length and open slightly posterior to the anus. These are about 1/2 the trunk length and the attachment membrane connective tissue may not be continuous along its entire length, but rather may be attached at intervals along the way. A single fixing muscle near the junction of the intestine and rectum may be present, and the spindle muscle is attached posteriorly. The rectum has a diameter that is less than the intestine and lacks a caecum. The retractor muscle comes from two origins, probably best described as a single retractor with two roots although it could be interpreted as two retractors that fuse. This latter is probably the case from what we know about the development of these organisms. However, to be consistent with the literature of this genus, it might be best to say a single retractor with two roots. These roots originate near, but not at, the posterior end of the trunk in a normal fashion.

In this subgenus there are two species that have been described as having one retractor with two roots, a posteriorly attached spindle muscle, and without hooks. It differs from both of these, that is *A. albus* and *A. venabulus*, in the angle at which the introvert comes off (40-45°) and also the nature of the shields which is quite different than both those two species.

The name is in honor of Dr. Bernard A. THOMASSIN who collected all but one of these specimens plus many others in this report as part of his studies on the biology of coral reefs.

The type material has been deposited in the Muséum national d'Histoire naturelle, Paris. Holotype : Cat. n° AH-406 ; BT Sta. 452 ; "devant labo., Ilo-Ilo, seagrass bed". Paratypes : Cat. n° AH-407 ; BT Sta. 419 ; "Récif de Songoritelo" ; Cat. n° AH-408 ; BT Sta. 136 ; "Grand Récif", Tuléar.

Aspidosiphon (Paraspidosiphon) angulatus (Ikeda, 1904)

Moorea BT Sta. 27, 18 spec.

Tuléar BT Sta. 678, 1 spec. seagrass bed on reef flat.

These 19 specimens with unidentate hooks (15-25 μm high) and retractor muscle origins in the third quarter of the trunk range in size from 3-27 mm (most less than 10 mm). The hooks are colorless and there is some variability in the angle at which the points are bent. The introvert is longer than the trunk. The anal shield has fewer than 10 longitudinal grooves dorsally which run into a compact central area and then become more diffuse and granular ventrally. The borders of this shield are not sharp as the hardened papillae become scattered and gradually decrease in size to merge with the trunk papillae. The caudal shield has about 25-30 radiating grooves. The transparent to off-white trunk usually allows the longitudinal muscle bands to be seen from the outside. These are not strongly developed even in the larger worms and as STEPHEN & EDMONDS (1972 : 241) point out, "longitudinal muscles incompletely divided into frequently anastomosing bundles."

The nephridia are about half as long as the trunk, attached for half to two thirds their length and open just posterior to the anus. No caecum was seen on the short rectum. The contractile vessel is simple and a strong spindle muscle anchors both ends of the gut coil. Most of these specimens were uncoiled, one larger one had lived in a scaphopod shell and only one had clearly inhabited a gastropod shell.

DISTRIBUTION. — The two existing records for this species are from the West Caroline Islands and Japan. The specimen from Sta. 678 represents the first Indian Ocean report for this form which appears to be another member of the Indo-West Pacific shallow water fauna.

Aspidosiphon (Paraspidosiphon) klunzingeri (Selenka, de Man & Bulow, 1883)

HOE Sta. 16; 1 spec.; 8/3/63; 21°02' N, 157°41' W; 48 m; Molokai, Hawaii. — 390S; 3 spec.; 9/9/64; 29°35' S, 31°42' E; 138 m; Durban.
Tuléar BT Sta. : 18, 1 spec.; 257, 1; 615, 2; 637, 1; 650, 1.
Fort-Dauphin, DECARY coll., 1932, 1 spec.

These 16 specimens were difficult to assign to this taxon. The alleged differences between *A. cumingii* and *A. klunzingeri* are not clearcut and the literature over the years has several inconsistencies. According to STEPHEN & EDMONDS (1972) *A. cumingii* has a rectal caecum and contractile vessel villi while *A. klunzingeri* does not. Also *A. cumingii* has 27-38 longitudinal muscle bands while *A. klunzingeri* has 38. However, earlier authors have reported contrary data and/or opinions, and the choice of this name for these organisms is somewhat arbitrary. It is hoped that a careful analysis of this complex can be made in the future (see also CUTLER, 1977).

Most of the worms are around 10-15 mm but range in trunk length up to 40 mm. Single-pointed hooks, measuring up to 70 μ m in the largest worm, are arranged in rows but are scattered more proximally. The dark brown anal shield has about 12 short grooves dorsally which degenerate to the coarse granular ventral region. The caudal shield has more grooves but otherwise is similar to the anal shield.

Internally the pair of retractor museles originate at the caudal shield and a spindle muscle anchors the gut coil at both ends. A rectal caecum is present. The nephridia are variable in position and attachment. In the 40 mm worm from Sta. 16, one nephridium is much shorter than the other and had a secondary lobe. This is considered to be an anomaly.

There are three specimens from Anton Bruun Sta. 390S which might be this species but their small size (4-6 mm) and our uncertainty caused us to refrain from making a positive identification.

DISTRIBUTION. — Except for one report from Durban, these are the first records from the southwestern Indian Ocean. It has been found in the northern and western part as well as the Red Sea, Funafuti, and the Great Barrier Reef. The Hawaii record is a new eastward extension. It has also been found on both sides of tropical Atlantic Ocean but not yet from the Eastern Pacific.

***Aspidosiphon (Paraspidosiphon) speculator* (Selenka, 1885)**

HOE "Te Vega" Sta. 45; 1 spec. — Sta. 45-4; 5 spec. 9/10/63; 6° 12' N, 155°37' E; 32 m; Bougainville Island, Solomons. — Sta. 45-8; 11 spec. 9/10/63; 6°12' N, 155°39' E; 2 m; Bougainville Island, Solomons. — Sta. 82 LH 10; 11/06/63; 9°26' N, 97°54' E; 1 m; Thailand. Tuléar PG Sta. 44; 1 spec. outer boulder reef tract. — BT Sta. : 154, 1 spec. : 240, 1 spec. ; 270, 1 spec. ; in coarse and gravelly sands.

The trunk length of these 22 worms range from 3-27 mm. The body wall is transparent except near the two ends in larger ones where it becomes thick and rough, leathery, almost corky looking. The granular or warty, ungrooved, smooth anal shield is gold to dark brown with moderately distinct borders, while the caudal shield is very indistinct and weakly chitinized.

The introvert, which is about as long as the trunk, bears rows of bidentate hooks but also has scattered unidentate hooks more proximally. The orientation of the hook on the slide could make it appear as a tetrahedron with a less sharply bent point as stated in STEPHEN & EDMONDS (1972). In their key to this taxon (p. 239) it is necessary to assume this species has only bidentate hooks.

Internally the anastomosing longitudinal muscle bands number around 24 or less. The two roots of the retractor muscle originate near the caudal shield and a strong spindle muscle anchors both ends of the gut coil. A rectal caecum is present and the wing muscles are well developed. The short nephridia are partially attached and open at or just posterior to the level of the anus.

DISTRIBUTION. — The two previous records for this species are from Cape Verde Islands and the Gulf of Guinea, so these Madagascar, Thailand, and Solomon Island worms represent a remarkable extension of the range in the western Indian and Pacific Oceans.

Aspidosiphon (Paraspidosiphon) steenstrupi Diesing, 1859

HIOE Sta. 407 I; 9 spec.; 10/14/64; 17°19' S, 43°14' E; 58 m; NW Majunga, Madagascar. — B-3; 3 spec.; 2/9/63; 12°00' S, 96°50' E; 1 m; Cocos-Keeling Islands; reef. — B-5; 2 spec.; 1/24/63; 12°00' S, 96°50' E; 1 m; Cocos-Keeling Islands; lagoon.

These are 14 representations of this wide spread species with double-pointed hooks and two retractor muscles originating in front of the caudal shield. The tightly packed rows of hooks have the small tubular papillae between them. The dark anal shield is granular or warty and may have chalky deposits on it. The ill-defined caudal shield has vague grooves on it.

DISTRIBUTION. — This species occurs in the Caribbean from Cuba to Brazil; Cape Verde Islands, South Africa, Red Sea, Mauritius, and several other Indian Ocean locations through Indonesia to Japan, Australia, and several West Pacific Islands. In other words, this is a circumtropical species except for the eastern Pacific.

Aspidosiphon (Paraspidosiphon) truncatus Keferstein, 1867

HIOE Sta. EC 21; 3 spec.; 8/22/64; 25°57' S, 33°02' E; 1 m; Inhaca Islands; rock.

These three worms range in trunk length from 7-18 mm and bear colorless, single-pointed hooks 25-35 μ m high in rows. The medium brown anal shield has distinct borders and has anastomosing grooves dorsally, becoming granular, with an area of cone-shaped spikes around where the introvert protrudes. The caudal shield is grooved and similar in color to the trunk which is thick walled. The pair of retractor muscles run the length of the body and the nephridia open at the level of the anus.

DISTRIBUTION. — The known range of this species has some peculiar gaps in it. It has been recorded in the Caribbean but not off West Africa. It occurs in the Red Sea, several places along the eastern African coast and Madagascar, then appears in Japan and the Sunday and Loyalty Islands. This collection from Mozambique fits in with a species which seems to inhabit only the western margins of three Oceans.

Aspidosiphon (Paraspidosiphon) ochrus n. sp.

HIOE Sta. 407 I; 4 spec.; 10/14/64; 17°19' S, 43°14' E; 58 m NW of Majunga, Madagascar; coral. — B-5; 2 spec.; 1/24/63; 12°00' S, 96°50' E; 1 m; Cocos-Keeling Islands; lagoon. — 45-4; 5 spec.; 9/10/63; 6°12' S, 155°37' E; 32 m; Bougainville Island, Solomons; coral. — HA 67-32; 2 spec.; 8/5/67; 7°21' S, 72°28' E; 1 m; Diego Garcia. Tuléar PG Sta. 4; 1 spec.; boulder reef tract.

This form has the typical *Aspidosiphon* appearance. The trunk size ranges from 9-20 mm in length and 1.5-5 mm in diameter. The introvert is approximately the same length as the trunk, perhaps slightly longer in some. At the tip are normal, small aspidosiphonid tentacles. Double-pointed hooks, arranged in 20-40 rings, are present. This area is usually followed by a more proximal region of scattered hooks. The height of the hooks in rings ranges from 36-50 μm . On some individuals, proximal to the hooked area, the introvert exhibits darkly pigmented bands or regions similar to some *Phascolosoma*. Between the rows of hooks one can find tubular cylindrical papillae approximately the same height as the hooks. No other papillae are seen on the introvert nor are there obvious papillae on the trunk (fig. 15).

The anal shield (fig. 16) is a striking creamy tan and paler than the surrounding brown trunk and with distinct, sharp boundaries. The shield is composed of uniform, densely-packed, wart-like units similar to *A. steenstrupi*. The caudal shield is much less distinct having ill-defined borders and being only slightly darker brown in color and thickened epidermis with radiating grooves. In a few specimens the central region of the posterior

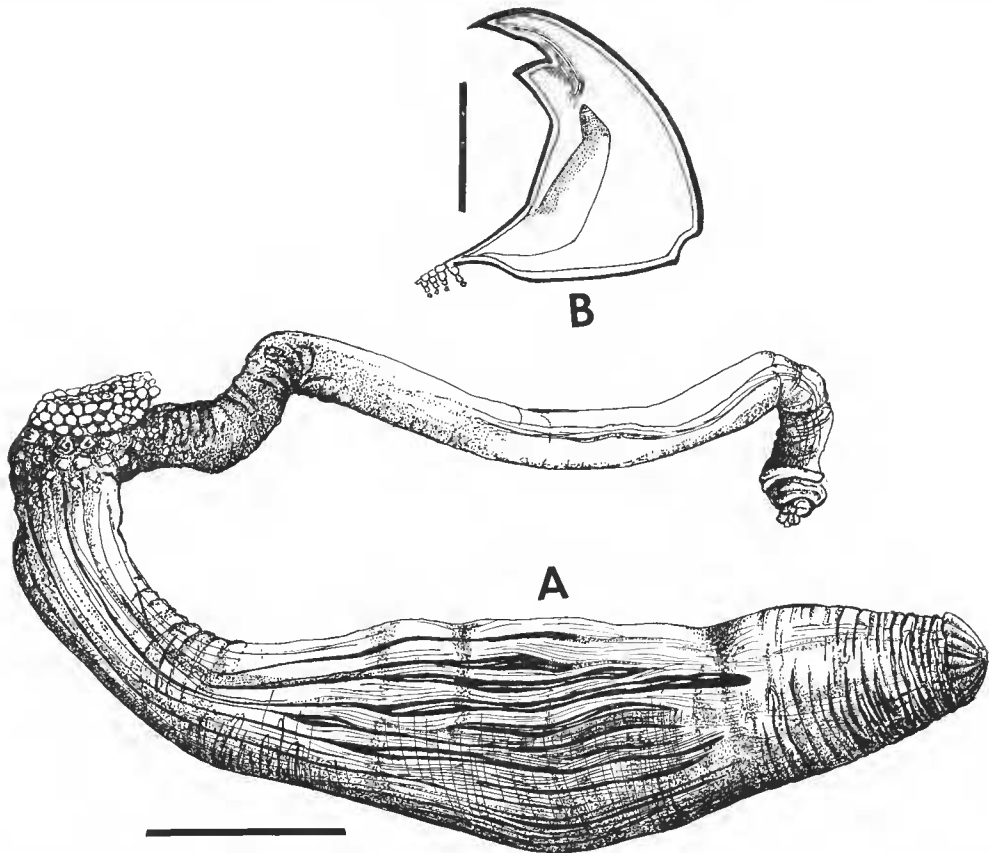


FIG. 15. — *Aspidosiphon ochrus* n. sp. : A, whole animal (scale = 3 mm) ; B, hook (scale = 20 μm).

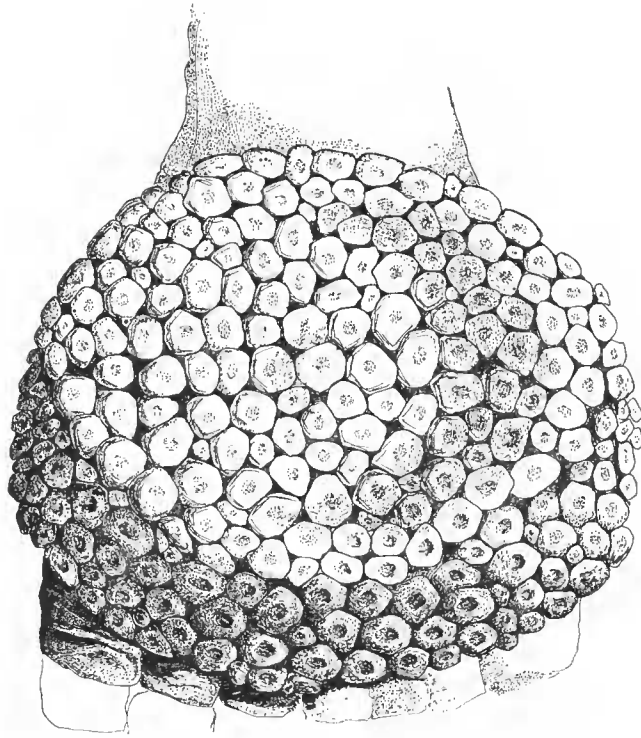


FIG. 16. — *Aspidosiphon ochrus* n. sp. Anal shield.

end of the trunk was withdrawn or sucked in forming a small depression. It gives the appearance of a calloused epidermis rather than a chitinous or calcareous structure (fig. 17).

Internally the intestine is anchored posteriorly by the spindle muscle. The rectum is fastened near the anus by a normal wing muscle; no caecum was observed. The nephridia are straight, about one half as long as the trunk, and are attached for most of their length to the body wall. The nephridiopores are slightly posterior to the anus. The pair of retractor muscles originate near the posterior end from broad bases spanning 5-8 longitudinal muscle bands, and are fused into a single muscle for about one half their length. The 25-30 longitudinal muscle bands anastomose frequently.

This new species with double-pointed hooks and two retractor muscles is closely related to *A. steenstrupi*. The most obvious distinction is the much paler anal shield. The name of this species is Greek for pale or light colored. The retractor muscles originate closer to the posterior end, there are more longitudinal muscle bands, and the nephridia are attached more completely.

The type material has been deposited in the Muséum national d'Histoire naturelle, Paris. Holotype: Cat. n° AH-404; "Anton Bruun" Sta. 407 I; NW Majunga, Madagascar. Paratypes: Cat. n° AH-405; "Te Vega" Sta. 45-4; Bougainville Island.

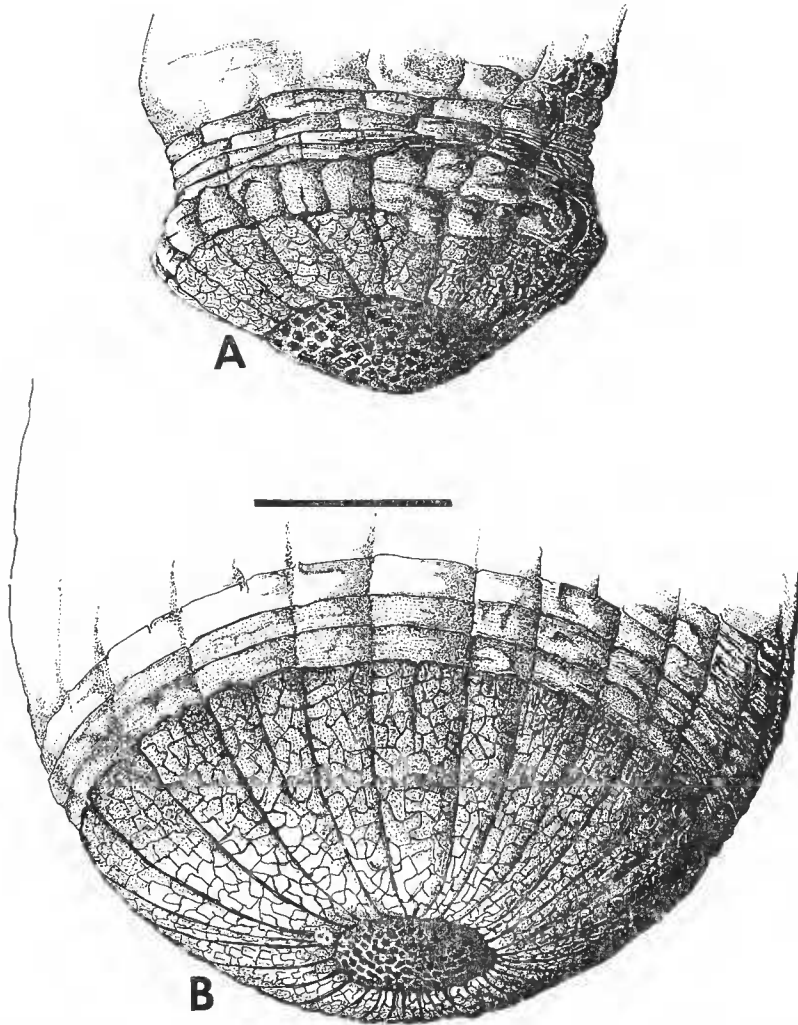


FIG. 17. — *Aspidosiphon ochrus* n. sp. Caudal shield : A, contracted state ; B, relaxed state.
(Scale = 1 mm.)

***Lithacrosiphon cristatus* (Sluiter, 1902)**

HOE Sta. 45-4 ; 1 spec. ; 9/10/63 ; 6°12' S, 155°37' E ; 32 m ; Bougainville Island, Solomons ; coral.

This 20 × 2 mm worm has its introvert completely withdrawn but both bidentate and unidentate hooks were observed. The nephridia are about 70 % of the trunk length and the anal shield is grooved. This species and related forms were discussed at length

in a recent review paper (CUTLER & JURCZAK, 1975) where it was redescribed and now includes *L. alticonus*, *L. gurjanovae*, *L. indicus* and *L. odhneri* as junior synonyms.

DISTRIBUTION. — This western Pacific record fits in with the known distribution pattern of this species which is somewhat unique. It is known from Brazil, the Caribbean, west coast of Panama, Hawaii, Gilbert Islands, Siapan, Timor, and Malaya but no further into the Indian Ocean; a western Atlantic and Pacific Ocean tropical species.

***Lithacrosiphon maldivensis* Shipley, 1902**

HIOE Sta. 407 I; 6 spec.; 10/14/64; 17°19' S, 43°14' E; 58 m; NW of Majunga, Madagascar; coral. — B-3; 2 spec.; 2/9/63; 12°00' S, 96°50' E; 1 m; Cocos-Keeling Islands; reef. — B-5; 1 spec.; 1/24/63; 12°00' S, 96°50' E; 1 m; Cocos-Keeling Islands; lagoon.

Only four of these have complete trunks and their length varies from 10-15 mm. Some of the others were apparently larger but this cannot be determined. All of these show the ungrooved, smooth, slightly granular anal shield characteristic of this species. Seven of these animals have been previously reported in CUTLER & JURCZAK (1975) where this genus was reviewed. The six worms from Sta. 407 I show an interesting transition from the smallest, whose anal shield has just a small dot of calcareous material on its tip, through intermediate size to large, which has a tall, smooth, cone-shaped mass of white material to the largest where this has itself become overgrown with other organisms, giving an irregular shape to it. HUGHES (1974) provides a detailed description of this species.

DISTRIBUTION. — These records from both sides of the Indian Ocean supplement the previous Indo-West Pacific records from the Red Sea, Maldivic Islands, Saipan, and Gilbert Islands.

***Cloeosiphon aspergillus* (Quatrefages, 1865)**

HIOE Sta. 407 I; 3 spec.; 10/14/64; 17°19' S, 43°14' E; 58 m; NW of Majunga, Madagascar; coral. — B-5; 1 spec.; 1/24/63; 13°00' S, 96°50' E; 1 m; Cocos-Keeling Islands; lagoon. — JR-18; 1 spec.; 12/30/63; 13°31' S, 48°20' E; 4 m; Nosy Bé. — 82 LH 10; 4 spec.; 11/6/63; 9°26' N, 97°54' E; 1 m; Thailand. — 87 LH 17; 3 spec.; 11/15/63; 7°40' N, 98°48' E; 1 m; Thailand.

Tuféar PG Sta. : Many specimens (380) collected in the rocky substrate on the outer boulder tracts.

These 420 worms of this well known and distinctive species vary in trunk length from 10-82 mm. The unique anal shield makes it possible to easily identify this species even when only an incomplete specimen is collected, which is true for many of these. It is only found in coral and is sometimes damaged in the extraction process.

DISTRIBUTION. — This species has been reported numerous times from throughout the Indo-West Pacific shallow water region.

Centrosiphon sp.

Tuléar BT Sta. : 222, 1 spec. ; 436, 1 ; 822, 1 ; in fine to coarse sands, on the deep part of the outer reef slope, on the lagoonal bottoms, and in the littoral terrigenous seagrass bed.

These unique worms seem to fit SHIPLEY's genus, but are not *Centrosiphon herdmani* (Shipley, 1903). His species had four retractors ; this has only a single pair, fused for most of their length and having their origins about a third of the distance from the anterior

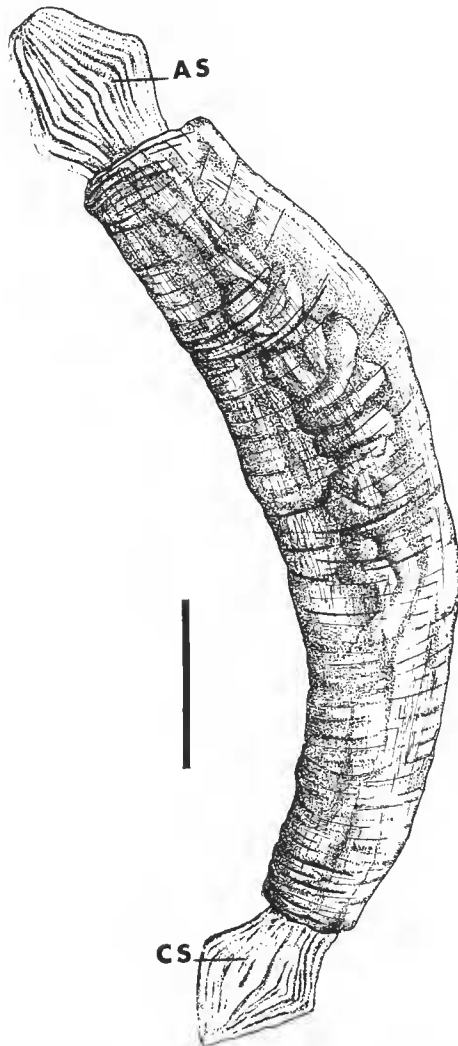


FIG. 18. — *Centrosiphon* sp. with introvert retracted. (Scale = 2 mm.)
AS = anal shield ; CS = caudal shield.

end of the trunk. The largest, light brown one from Sta. 436 has a trunk 10×2 mm and the introvert, while withdrawn, is 1.5-2 times this length. The skin has faint transverse and longitudinal lines on its surface. The trunk of the smallest one, from Sta. 822, is 4×1 mm and transparent. There are dark hooks in 15-20 rows which are about 30-40 μ m in height. Digitiform tentacles are present and number around 20. The worm from Sta. 222 has a 5 mm trunk and an 8 mm introvert and is in poor condition.

Internally the coiled gut is not anchored posteriorly by the spindle muscle and a rectal caecum is present. The pair of short nephridia are attached to the body wall for about one half their length and open slightly anterior to the anus. The contractile vessel is simple.

The character which forces us to place these specimens in this all but forgotten taxon (there have been no reports since SHIPLEY'S original record over 70 years ago and his type material cannot be located) is the nature of the anal shield and the fact that the introvert protrudes through the center. Both shields consist of smooth, hardened, chitinous material subdivided by narrow grooves or furrows. The 10 mm worm has about 34 grooves in the caudal shield and 28 in the anal shield. These structures have distinct borders where they meet the trunk and both, while obviously flexible, have the general form of two broad cones fused at the large end (fig. 18).

Phascolosoma (Satonus) pectinatum Keferstein, 1867

Tuléar BT Sta. 124; 1 spec. outer boulder reef tract.

This unique species with bilobed nephridia and spinelets on the base of the pale introvert hooks is represented by only a single worm whose trunk is 22 mm long. The longitudinal muscle bands are not strong and anastomose frequently, the spindle muscle is not attached posteriorly, the retractor muscles are rather thin, and the coelom is packed with sperm.

DISTRIBUTION. — The known distribution of this species includes the Caribbean, Azores, Mauritius, Surinam, Tasman Sea, East China Sea, southern California and Panama in the eastern Pacific, so this is only the second record from the Indian Ocean of what may be an uncommon circumtropical species.

Phascolosoma (Phascolosoma) agassizii Keferstein, 1867

HOE Sta. : KA 13; 1 spec. ; 1/22/64 ; 11°45' S, 42°15' E ; 1 m ; Grand Comore Island. HA 67-40 ; 2 spec. ; 7/10/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia.

These three small specimens have trunks 8-14 mm long and are thick skinned with papillae uniformly distributed over their surface. The hooks are about 50 μ m high and notched on the concave side in a manner which sometimes almost gives the appearance of a bidentate hook. There are 23 or 24 longitudinal muscle bands, a posteriorly attached

spindle muscle and the nephridia, which are about 2/3 attached, open just posterior to the anus.

DISTRIBUTION. — There are several reports from West Africa and then around Cape Province, Durban, several Indian Ocean records, Indo-China, Australia, and then along the Pacific coast of the United States. It seems to be absent from the western Atlantic Ocean and Central American waters.

Phascolosoma (Phascolosoma) albolineatum Baird, 1868

HOE Sta. : HA 67-40 ; 20 spec. ; 7/10/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia. — HA 67-46 ; 6 spec. ; 7/18/67 ; 7°22' S, 72°29' E ; 1 m ; Diego Garcia.

These 26 pale worms have trunks varying in length from 11-48 mm and many have gametes in the coelom. The introvert is about half the trunk length, carries dark red papillae proximally and bears rows of hooks with strongly bent points. The clear streak in these hooks varies in length, often being shorter than that illustrated in STEPHEN & EDMONDS (1972 : fig. 33A). Internally the nephridia open at the level of the anus, are a little less than half the trunk length and often attach for less than half their length, not three-fourths as earlier noted.

The unique feature in this population is the retractor muscles : there are two, three, and four muscles in different animals. The normal condition is two pairs in which the dorsal muscle is smaller and shorter than the ventrals and quickly merge with the ventral muscle on the same side. It is apparent that this fusion becomes complete on one or both sides in some worms with the resultant loss of a separate dorsal retractor muscle. A similar situation was described by GIBBS (1973) in a population of *Golfingia rimicola*. This occasional occurrence of an anomalous condition does not necessitate the creation of a new taxon.

DISTRIBUTION. — The earlier records from the Indian Ocean are from Natal and Amboina. It has also been recorded from Java, Indo-China, Japan, and a few West Pacific Islands, so this record reinforces its shallow water, Indo-West Pacific character.

Phascolosoma (Phascolosoma) funafutiense (Fischer, 1914)

HOE Sta. : HA 67-40 ; 14 spec. ; 7/10/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia.
MC Sta. : 11 ; 4 spec. ; 8/14/70 ; 11°21' N, 162°22' E ; 1 m ; Eniwetok. — 13 ; 3 spec. ; 9/30/70 ; 11°21' N, 162°22' E ; 1 m ; Eniwetok.

These pale specimens seem to fit this uncommon species. The peculiar hook structure (STEPHEN & EDMONDS, 1972 : fig. 37C) with the small toe-like plates at the posterior base are quite distinctive. These populations range in trunk length from 11-70 mm. The nephridia open at the level of the anus and are as long as the trunk. There are four retractor muscles. The dorsal pair originate 2/3 the distance to the posterior of the trunk and

the ventral pair originate $3/4$ of the distance. This is further posterior than previously noted.

DISTRIBUTION. — The two previous records are from Funafuti and the Christmas Islands, so this Diego Garcia record constitutes a westward extension into the Indian Ocean.

Phascolosoma (Phascolosoma) nigrescens Keferstein, 1865

HOE Sta. B-4; 1 spec.; 2/7/63; 12°00' S, 96°50' E; 4 m; Cocos-Keeling Island; reef. — EC 21; 1 spec.; 8/22/64; 25°57' S, 33°02' E; 1 m; Inhaca Island; rock. — RU 271 & 152; 2 & 4 spec.; 11/22/64; 11°40-47' S, 43°16' E; 2-3 m; Grand Comore Island. — 18 A; 3 spec.; 3/21/63; 7°35' N, 98°08' E; 74 m; SW of Sumatra. — 47 B; 2 spec.; 4/5/63; 19°50' N, 92°55' E; 26 m; Bay of Bengal. — 372 P & D; 4 spec.; 8/19-22/64; 25°50' S, 34°49' E; 19-37 m; South Mozambique. — 381 A & B; 2 spec.; 8/19-22/64; 33°13' S, 43°51' E; 38-46 m; S. of Madagascar. — 407 I; 1 spec.; 10/14/64; 17°19' S, 43°14' E; 58 m; NW Majunga, Madagascar. — 447, 449, 453; 10 spec.; 12/16/64; 10°-11°11' N, 51°15' E; 35-60 m; Somalia-Gulf of Aden. — HA 67-32; 7 spec.; 8/5/67; 7°21' S, 72°28' E; 1 m; Diego Garcia.

18 stations by J. RUDLOE; 98 spec.; 12/19/63-2/7/64; approx. 13°25' S, 48°20' E; 1-4 m; Nosy Bé, Madagascar.

Nosy Bé BT Sta. : 560, 2 spec.; *Enhalus acoroides* seagrass bed.

Tuléar PG Sta. : 35, 1 spec.; 39, 1; outer reef boulder tracts. — BT Sta. : 20 spec. in 14 sta. distributed on the reef slopes and flats.

Fort-Dauphin, DECARY coll., 1932 : 6 spec.

This widely distributed species is represented by 180 specimens ranging in trunk length from 1.5-70 mm, most between 20 and 40 mm. In a few of the very smallest ones (2-3 mm) the bands or bundles of longitudinal muscles are extremely difficult to discern. STEPHEN & EDMONDS (1972 : 317) commenting about longitudinal muscle bands in *P. pacificum* said, "... except in very young specimens where they may be continuous." So, it is possible that these have not developed yet. RICE (1973 : 6) while describing the development of *P. agassizii* says : "The adult arrangement of longitudinal muscles into bundles of fibers is not discernable in the larva." It seems logical to assert that this important character has not yet appeared in the 2 and 3 mm animals in our collection. Therefore, if generic features are not visible at this stage, species characters are probably undeveloped also. In these very small worms the introvert is shorter than the trunk. These worms have the spindle muscle attached posteriorly, nephridia which are about half attached and open at the same level as the anus.

A final note about hook size and the clear streak. In CUTLER (1965) this was discussed and the conclusion was reached that the hook size was variable but not in direct proportion to trunk length (CUTLER, 1965 : fig. 5). The size range of the specimens analyzed was from 25-100 mm and hook height from 48-92 μ m. This recent collection allowed us to extend that analysis to the lower size ranges (1.5-5 mm). This is shown in figure 19. The smaller animals clearly have smaller hooks (about 20-30 μ m). It now looks as if the hook size increases rapidly while the worm grows to 30 or 40 mm, levels off at a plateau around 65-75 μ m until the worm exceeds 80 mm, and then increases to around 90 μ m. This apparent second growth spurt in larger worms may be unreal. A most interesting contribution

has recently been made by BERTSCH (1976) wherein he describes ontogenetic radular variation in opisthobranchs and arrives at very similar conclusions from very similar data.

The fixed, absolute character of the clear streak in these hooks is inaccurate. One can find on many worms, upon careful examination of a large number of hooks, at least a few in which there is a suggestion of a separation of a triangular area at the anterior basal region, similar to that found in *P. scolops*.

DISTRIBUTION. — This is a common circumtropical shallow water species. These records firmly establish its wide presence throughout the Indian Ocean.

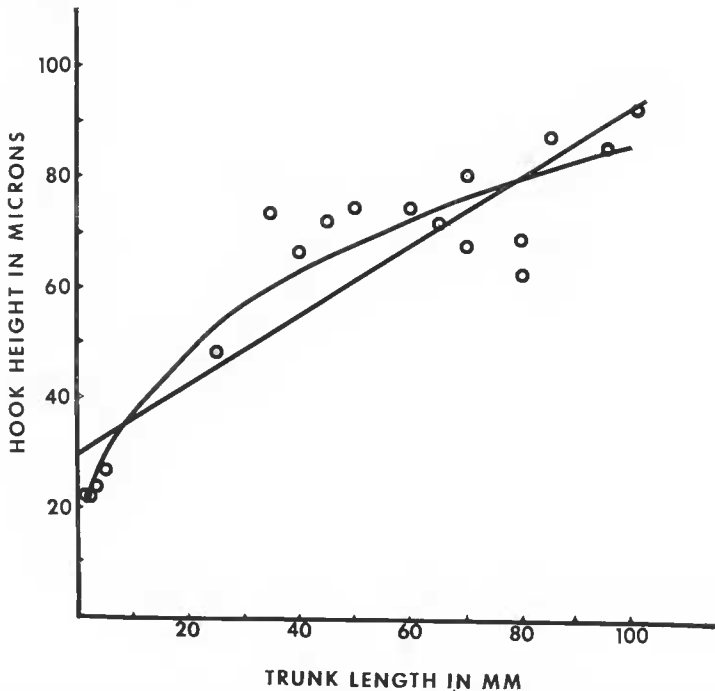


FIG. 19. — *Phascolosoma nigrescens*. Relationship between trunk and hook size. Calculating a simple linear regression ($Y = A + BX$) from these data one finds a positive slope of 0.62. However, after fitting several curves, the best fit (index of determination of 0.95) is a power function $Y = A + X^B$.

***Phascolosoma* (*Phascolosoma*) *pacificum* Keferstein, 1866**

IIOE Sta. : HA 67-32 ; 10 spec. ; 8/5/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia. — HA 67-40 ; 4 spec. ; 7/10/67 ; 7°21' S, 72°28' E ; 1 m ; Diego Garcia. — HA 67-48 ; 1 spec. ; 7/20/67 ; 7°17' S, 72°28' E ; 1 m ; Diego Garcia. — HA 67-52 ; 1 spec. ; 7/24/67 ; 7°19' S, 72°29' E ; 1 m ; Diego Garcia.

MC Sta. 11 ; 2 spec. ; 8/14/70 ; 11°21' N, 162°22' E ; 1 m ; Eniwetok. — 12 ; 1 spec. ; 8/28/70 ; 11°21' N, 162°22' E ; 1 m ; Eniwetok. — 14 ; 1 spec. ; 9/30/70 ; 11°21' N, 162°22' E ; 1 m ; Eniwetok.

Tuléar PG Sta. : 25 spec. collected in 8 stations on the outer, reef boulder tracts. — BT Sta. : 4 spec. sampled in 3 stations in the same biotope.

These 49 worms, ranging in trunk length from 25-125 mm, show 35-40 longitudinal muscle bands, the hook structure, long attached nephridia, and strong spindle muscle typical for this species. Most distinctive is the uniform distribution of large, cone-shaped papillae on the trunk (fig. 20). Our observations on the nephridial opening just anterior to the anus and the lack of a rectal caecum support those of EDMONDS (1956). One of our worms showed peculiar orange swellings along the esophagus. Another one exhibits an interesting feature where some of the hooks are evidently worn down and the clear streak goes out the top, suggesting that these were used for abrasion. Some of the larger hooks (105-125 μm) show a peculiar bubble-like clear blob rising up from the basal clear area and the triangular clear area varied in size (fig. 21). This variety can be seen from a single worm in the same row of hooks.

DISTRIBUTION. — Many reports of this species clearly show it to be a wide-spread member of the Indo-West Pacific shallow water family but not as numerous as some other members of this genus. It has previously been found in Madagascar. A single report (HALDER, 1975 : 60) from 400-800 m is unusually deep for this species.

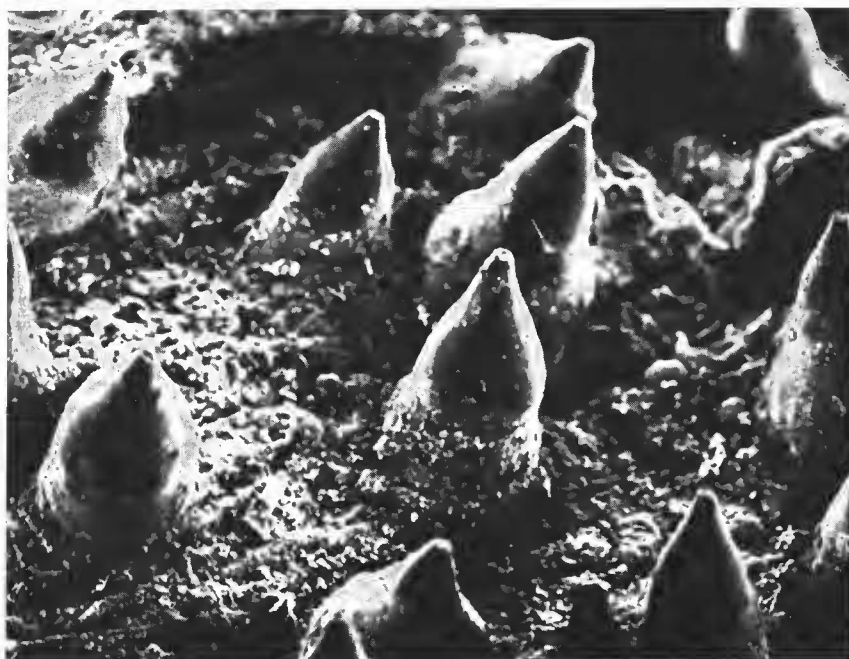


FIG. 20. — *Phascolosoma pacificum*. Papillae from mid trunk.
(Scanning electron micrograph 100 \times .)

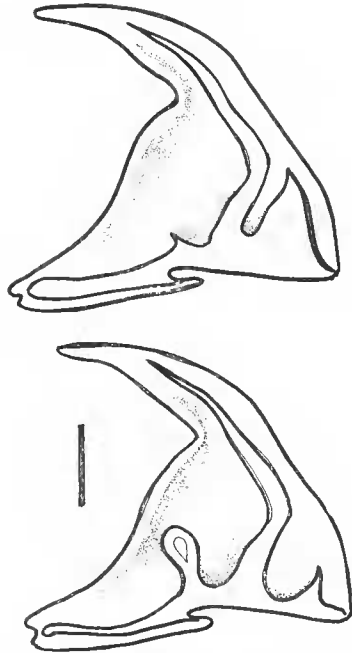


FIG. 21. — *Phascolosoma pacificum*. Introvert hooks showing variation of internal structure. (Scale = 30 μ m.)

***Phascolosoma* (*Phascolosoma*) *perlucens* Baird, 1868**

Tuléar PG Sta. : 37 spec. collected in 15 stations on the outer reef boulder tracts.

These 37 worms are in varying states of wholeness so sizes could not be accurately determined. They ranged up to 45 mm but many had their trunks damaged during their extraction from the coral. The large, posteriorly directed, preanal papillae and pale trunk make them easy to identify. Once again the supposedly characteristic triangular clear space in the hook varies in size and shape. This species was formerly known as *P. dentigerum*.

DISTRIBUTION. — This appears to be a circumtropical species but relatively uncommon in the Indian Ocean. It has been previously reported from Madagascar.

***Phascolosoma* (*Phascolosoma*) *scolops* Selenka, de Man & Bulow, 1883**

HOE Sta. "Te Vega" 16; 2 spec.; 8/3/63; 21°02' N, 157°41' W; 48 m; Maolikai, Hawaii. — "Te Vega" 92 LII 20; 1 spec.; 11/18/63; 7° 46' N, 98°21' E; 1 m; Thailand. — EC 21; 5 spec.; 8/22/64; 25°57' S, 33°02' E; 1 m; Inhaca Island. — RU 242; 2 spec.; 11/14/64;

4°05' S, 39°40' E; 1 m; Mombassa. — 28A; 2 spec.; 3/27/63; 11°52' N, 95°50' E; 62 m; NE Nicobar Island. — 206A; 44 spec.; 11/15/63; 20°33' N, 70°09' E; 43 m; NW of Bombay. — 269C; 11 spec.; 12/3/63; 23°35' N, 58°49' E; 122 m; Gulf of Oman. — 270A; 2 spec.; 12/4/63; 22°07' N, 59°48' E; 56 m; Gulf of Oman. — 372C, P & Q; 8 spec.; 8/19-22/64; 25°57' S, 33°00'-34°50' E; 22-42 m; South Mozambique. — 381B; 8 spec.; 8/27/64; 33°13' S, 43°51' E; 38 m; S. of Madagascar. — 400C; 15 spec.; 10/3/64; 20°00' S, 35°42' E; 62 m; Beira, Mozambique. — 453, 456; 2 spec.; 12/17/64; 11°11-14' N, 51°8-14' E; 29-48 m; Somalia. — HA 67-32 & 67-40; 41 spec.; 8/5/67 & 7/10/67; 7°21' S, 72°28' E; 1 m; Diego Garcia. 12 stations by J. RUDLOE; 24 spec.; 12/19/63-1/15/64; approx. 13°25' S, 48°20' E; 1-15 m; Nosy Bé, Madagascar.
 Tuléar: PG Sta.: 30 spec. sampled in 10 sta. on the outer reef boulder tracts. — BT Sta.: 17 spec. collected in 9 stations in coarse sediments, more frequently on the outer reef boulder tracts and on the bottoms of the outer reef creeks and sometimes on the outer reef slope.
 Fort-Dauphin, DECARY coll., 1932: 12 spec.

This most common member of the genus is represented by 227 specimens ranging in trunk length from 1.5-36 mm, most being around 10-15 mm and, therefore, generally smaller than *P. nigrescens*. It also differs externally by having a paler overall color and redder papillae. The clear triangular space at the base of the hook is usually distinctive. The clear streak running down the hook from its apex may vary somewhat in size and shape from hook to hook, not all being straight and of uniform width. The relationship between trunk and hook size seems to closely parallel the picture for *P. nigrescens*: the 2-5 mm worms having hooks about 20-30 μ m high and then increasing up to 50-70 μ m in a 25 mm worm. In the small ones e.g., those from Sta. 206A, the hooks are thin and pale, one 1.5 mm worm having only three rows of hooks.

Most of these animals have an introvert 1.5-2 times the trunk length which often has reddish brown pigmented blotches on a pale background. A few of the smallest worms (less than 5 mm) bear introverts a little shorter than the trunk. The nephridia are about half as long as the trunk or shorter in very young ones, open near the anus and are attached to the body wall for about half their length. A few of those from GALENON'S (PG) stations resemble the subspecies *mossambiciense* having curved dark lines in the hook.

DISTRIBUTION. — This species is known from throughout the tropical seas except for the eastern Pacific. The one station near Hawaii ("Te Vega 16") is therefore of interest. The other records reaffirm its widespread presence in shallow water throughout the Indo Pacific.

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Essai de classification de la sous-famille des Camallaninae (Nematoda, Camallanidae)

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Résumé. — Cinq genres sont reconnus dans la sous-famille : *Paracamallanus*, *Camallanus*, *Oncophora*, *Serpinema* et *Camallanides*. Toutes les espèces dont la hauteur de l'arrière-cavité buccale mesure plus du tiers de la longueur des valves sont placées dans le genre *Paracamallanus* qui réunit ainsi les espèces les plus primitives qui sont à la base des différentes lignées. Une liste des espèces, classées suivant leurs affinités morphologiques, est présentée. Les différents caractères du groupe sont analysés en fonction de leur valeur évolutive. Des conclusions sont présentées sur la paléobiogéographie de la sous-famille.

Abstract. — Five genera are recognized in the sub-family Camallaninae : *Paracamallanus*, *Camallanus*, *Oncophora*, *Serpinema* and *Camallanides*. All the species whose length of posterior part of buccal cavity measures more than a third of the valves length are placed in the genus *Paracamallanus*. This genus then groups the most primitive species which are at the origin of the different evolutionary lines. A list of the species, classified according to their morphological affinities, is presented. The different characteristics of the group are analysed in relation to their evolutive value. Conclusions are presented regarding the paleobiogeography of the subfamily.

INTRODUCTION

La sous-famille des Camallaninae groupe les Camallanidae à capsule buccale séparée en deux valves.

Suivant la classification de CHABAUD (1975), elle comprend cinq genres : *Paracamallanus*, *Camallanus*, *Oncophora*, *Serpinema* et *Camallanides*, les genres *Zeylanema* Yeh, 1960, et *Neocamallanus* Ali, 1956, n'étant pas reconnus.

Dans un travail précédent (PETTER, 1978), nous avons suivi cette classification, en considérant que la présence d'une arrière-cavité buccale (g. *Paracamallanus*) était plus importante au point de vue phylogénique que l'existence de denticulations sur les crêtes de la capsule buccale (g. *Zeylanema*) et l'absence de tridents (g. *Neocamallanus*), et devait donc avoir priorité sur ces caractères.

En fait, nous adoptons ainsi une classification horizontale, en plaçant dans le même genre toutes les espèces les plus primitives qui sont à la base des différentes lignées ; en passant en revue l'ensemble des espèces, nous avons constaté en effet que dans la région indo-malaise, où s'est effectuée l'évolution du groupe, les espèces pourvues de crêtes denticulées et celles pourvues de tridents constituaient de courts rameaux évolutifs avec à la

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base des espèces à arrière-cavité buccale développée et au sommet des espèces à arrière-cavité réduite à un mince anneau chitinoïde (fig. 4).

L'individualisation de lignées qui permettrait l'établissement d'une classification verticale se révèle cependant difficile car on observe une évolution en mosaïque, avec toutes les combinaisons de caractères représentées ; nous préférons donc conserver le genre *Paracamallanus*.

Nous avons en 1978 redéfini le genre en y plaçant les espèces dont la longueur de l'arrière-cavité buccale mesure plus du tiers de la longueur des valves. Bien que cette division ait l'inconvénient de placer dans des genres différents des espèces voisines qui sont à la limite entre les deux genres, elle nous paraît séparer dans l'ensemble deux groupes d'espèces correspondant à deux niveaux évolutifs différents ; nous avons constaté qu'un autre caractère, le nombre des papilles pré-cloacales, confirme la plupart du temps cette séparation.

Les genres peuvent alors être séparés par le tableau dichotomique suivant :

- 1 (2) Capsule buccale pourvue d'une arrière-cavité dont la hauteur mesure plus du tiers de la longueur des valves..... g. *Paracamallanus*
- 2 (1) Capsule buccale munie en arrière des valves d'un anneau chitinoïde dont la hauteur ne dépasse pas le tiers de la longueur des valves.
- 3 (8) Valves buccales dépourvues en leur milieu d'épaississement longitudinal externe. Tridents présents ou absents.
- 4 (7) Crêtes longitudinales de la capsule buccale non séparées en un groupe ventral et un groupe dorsal.
- 5 (6) Crêtes longitudinales de la capsule buccale non nettement divisées en un groupe antérieur et un groupe postérieur. Femelle mûre non brusquement élargie en dessous de la vulve. g. *Camallanus*
- 6 (5) Crêtes longitudinales de la capsule buccale divisées en un groupe antérieur et un groupe postérieur, ce dernier constitué par des rangées d'épines ou des crêtes courtes. Femelle mûre brusquement élargie en arrière de la vulve. g. *Oncophora*
- 7 (4) Crêtes longitudinales de la capsule buccale séparées en un groupe ventral et un groupe dorsal. g. *Serpinema*
- 8 (3) Valves buccales pourvues en leur milieu d'un épaississement longitudinal externe. Tridents remplacés par des baguettes simples. g. *Camallanides*

Comme nous l'avons fait dans un travail précédent pour la sous-famille des Procamallaninae (PETTER, 1979), nous avons essayé de présenter pour chaque genre une liste des espèces en les groupant suivant leurs affinités, afin de dégager les grandes lignes de l'évolution de la sous-famille.

LISTE DES ESPÈCES

N'ayant pas examiné nous-même les spécimens-types, nous avons préféré citer toutes les espèces décrites : de nombreuses synonymies sont certainement à établir dans cette liste, en particulier chez les espèces indo-malaises. Il ne s'agit donc pas d'une révision systématique au niveau spécifique.

- I. Genre *Paracamallanus* Yorke et Maplestone, 1926 (= *Neocamallanus* Ali, 1956, *pro parte* ; = *Zeylanema* Yeh, 1960, *pro parte*).

Genre caractérisé par une arrière-cavité buccale dont la hauteur mesure plus du tiers de la longueur des valves. Nombre des papilles pré-cloacales généralement de 5 paires. Parasites de Poissons d'eau douce en Asie tropicale et en Afrique.

A. Capsule ornée de crêtes longitudinales lisses, au nombre de 8 à 13. Tridents présents. Parasites de Siluriformes.

Parasite de Clariidae en Afrique.

— *P. cyathopharynx* (Baylis, 1923) (= *P. senegalensis* Vassiliades, 1970); espèce redécrite récemment par MORAVEC, 1974.

Parasites de Clariidae et Siluridae en Asie tropicale.

— *P. ceylonensis* (Fernando et Furtado, 1963).

— *P. longitridentatus* (Fernando et Furtado, 1963).

— *P. equispiculus* (Sood, 1968).

— *P. furtadoi* Petter, 1978.

B. Capsule ornée de crêtes longitudinales lisses, au nombre de 12 à 25. Tridents rudimentaires ou absents. Parasites de Channidae en Asie tropicale.

— *P. ophicephali* (Pearse, 1933); la femelle est redécrite par KARVE, 1941.

— *P. singhi* (Ali, 1956); espèce redécrite par KHAN et YASEEN, 1969.

— *P. yehi* (Fernando et Furtado, 1963).

— *P. bengalensis* (Soota et Chaturvedi, 1971); l'espèce est mise en synonymie avec *Camallanus atridentus* Khera, 1954, par SAHAY, 1972; cette synonymie ne nous paraît pas valable car *C. atridentus* a une arrière-cavité buccale beaucoup moins développée et un anneau de fines dents à la base de la capsule.

C. Capsule ornée de crêtes longitudinales denticulées. Tridents présents ou absents. Parasites de Channidae en Asie tropicale.

1. Crêtes longitudinales au nombre de 9. Tridents présents.

— *P. sweeti* (Moorthy, 1937).

2. Crêtes longitudinales au nombre de 16. Tridents absents.

— *P. maculati* (Ila Ky, 1971).

II. Genre *Camallanus* Railliet et Henry, 1915 (= *Neocamallanus* Ali, 1956, *pro parte*; = *Zeylanema* Yeh, 1960, *pro parte*).

Genre caractérisé par une arrière-cavité buccale réduite à un anneau chitinoïde dont la hauteur ne dépasse pas le tiers de la longueur des valves. Crêtes longitudinales de chaque valve buccale non séparées en deux groupes. Nombre des papilles pré-cloacales généralement de 6 à 7 paires. Parasites de Poissons et d'Amphibiens anoures.

A. Capsule ornée de crêtes longitudinales denticulées, au nombre de 7 à 12 (le plus souvent 9). Parasites de Poissons d'eau douce (Mastacembelidae et Anabantidae principalement) en Asie tropicale et en Afrique et de Ranidae en Asie tropicale.

1. Tridents présents.

Parasites de Poissons d'eau douce en Asie tropicale.

Plusieurs de ces espèces ont une arrière-cavité buccale relativement développée, et peuvent être considérées comme intermédiaires entre les genres *Paracamallanus* et *Camallanus*.

— *C. anabantis* Pearse, 1933, *pro parte* ; espèce redécrite par CHAKRAVARTY, 1939, KULASIRI et FERNANDO, 1956, YEH, 1960, FERNANDO et FURTADO, 1963 *a* et *b*, et PETTER, 1978.

— *C. unispiculus* Khera, 1954 ; l'espèce est mise en synonymie avec *C. anabantis* par YEH, 1960, synonymie réfutée par AGRAWAL, 1967.

— *C. mastacembeli* (Sahay et Sinha, 1966) (= *C. patani* Sood, 1968).

— *C. sp.* Agrawal, 1967 (= *C. mastacembeli* sensu Agrawal, 1967, et Sood, 1968).

— *C. magna* (Khan et Yaseen, 1969).

— *C. spinosa* (Furtado, 1965) ; espèce redécrite par PETTER, 1978 ; caractérisée par la présence de 4 rangées longitudinales d'épines cuticulaires.

Parasite d'Anabantidae africains.

— *C. ctenopomae* Vassiliades et Petter, 1972.

Parasites de Ranidac en Asie tropicale.

— *C. thapari* Gupta, 1959.

— *C. nodulosus* Gupta, 1959.

— *C. inglisi* Agrawal, 1967.

— *C. mujibia* (Bashirullah et Khan, 1972).

2. Tridents absents. Parasites de Poissons d'eau douce en Asie tropicale.

Espèces à arrière-cavité buccale relativement développée, pouvant également être considérées comme intermédiaires entre *Paracamallanus* et *Camallanus*.

— *C. pearsei* (Yeh, 1960) (= *C. anabantis* Pearse, 1933, femelle) ; espèce redécrite par YEH, 1960, et FERNANDO et FURTADO, 1963*b*.

— *C. kulasirii* (Yeh, 1960).

B. Capsule ornée de crêtes longitudinales lisses.

1. Tridents absents. Nombre des crêtes longitudinales supérieur à 12. Parasites de Poissons d'eau douce en Asie tropicale.

Espèces à arrière-cavité buccale relativement développée.

— *C. trichogasterae* Pearse, 1933.

— *C. atridentus* Khera, 1954 ; espèce redécrite par SAHAY, 1968 ; caractérisée par la présence d'un anneau de fines dents à la base de la capsule buccale.

— *C. xenentodoni* Khan et Yaseen, 1969 ; espèce caractérisée par des crêtes longitudinales très courtes et limitées aux bords supérieurs de la capsule buccale.

— *C. salmonae* Chakravarty, 1942 ; espèce insuffisamment décrite, d'affinités douteuses.

2. Tridents présents.

a — Parasites de Poissons.

α. Crêtes longitudinales au nombre de 9. Parasites de Chaenidae en Asie tropicale.

— *C. fernandoi* (Yeh, 1960) ; espèce à arrière-cavité buccale relativement développée ; caractérisée par la présence d'une dent postérieure sur chacune des 7 crêtes longitudinales médianes.

— *C. thaparus* Sahay et Narayan, 1968.

β. Nombre des crêtes longitudinales au moins égal à 12.

• Queue de la femelle arrondie à l'extrémité et longue d'au moins 450 μm. Vulve généralement médiane ou postérieure au milieu du corps. Parasites de Poissons d'eau douce, principalement Cypriniformes.

Parasites de Cypriniformes et Cyprinodontiformes (Poissons d'élevage) en Asie tropicale.

— *C. fotedari* Raina et Dhar, 1972.

— *C. moravecii* Petter, Cassone et France, 1974 ; espèce trouvée en France chez des Cyprinodontiformes provenant d'un élevage de Singapour.

Parasite de Poissons d'eau douce (principalement Cypriniformes) en Asie orientale.

— *C. cotti* Fujita, 1927 (= *C. zacconis* Li, 1941) ; espèce redécrite par YAMAGUTI, 1941, et STUMPP, 1975.

Parasites de Poissons d'eau douce variés en Amérique du Nord.

— *C. ancylodirus* Ward et Magath, 1916.

— *C. oxycephalus* Ward et Magath, 1916 ; redécrite par STROMBERG, SUEGOG et CRITES, 1973.

Parasites de Cypriniformes africains.

— *C. kirandensis* Baylis, 1928.

— *C. longicaudatus* Moravec, 1973.

• Queue de la femelle inférieure à 450 μm ou munie de 2 à 3 pointes terminales.

Parasites de Poissons d'eau douce (principalement Percidae) dans la région paléarctique. Queue de la femelle comprise entre 200 μm et 1,01 mm et munie de 2 à 3 pointes terminales. Vulve généralement légèrement postérieure au milieu du corps.

— *C. lacustris* (Zoega, 1876) (= *C. wolgensis* Lewaschov, 1929)¹ ; récemment redécrite par MORAVEC, 1969 et 1971.

— *C. truncatus* (Rudolphi, 1814) ; redécrite par TÖRNQUIST, 1931, MEZAROS, 1967, et MORAVEC, 1971.

Parasites de Poissons marins dans les océans Indien et Pacifique. Queue de la femelle inférieure à 450 μm, munie ou non de 2 à 3 pointes terminales. Vulve souvent proéminente et antérieure au milieu du corps.

— *C. carangis* Olsen, 1954.

— *C. marinus* Schmidt et Kuntz, 1969.

1. Pour la liste complète des synonymes de *C. lacustris*, voir IVASHKIN, SOBOLEV et KIROKOVA, 1971.

- *C. chorinemi* Rasheed, 1970.
- *C. surmai* Rasheed, 1970.
- *C. indicus* Kalyankar, 1971.
- *C. karachiensis* Khan et Begum, 1971.
- *C. cinereusis* Bilqees, Khanum et Jehan, 1971.
- *C. magnavaginus* Bilqees, Khanum et Jehan, 1971.
- *C. trichiuris* Bashirullah et Rahman, 1972.
- *C. puriensis* Srivastava et Gupta, 1977.
- *C. pentkotai* Srivastava et Gupta, 1976.
- *C. trichiurusi* Srivastava et Gupta, 1976.

Parasite d'Ostéoglossiformes au Brésil. Queue de la femelle inférieure à 450 μm . Vulve légèrement postérieure au milieu du corps.

— *C. tridentatus* (Drasche, 1884) ; redécrite par BAYLIS, 1927 et TRAVASSOS, ARTIGAS et PEREIRA, 1928.

- Longueur de la queue chez la femelle inconnue.

Parasite de Cyprinidae en URSS.

- *C. hypopthalmichthys* Achmerov, 1954 ; décrite par DOGIEL et ACHMEROV, 1959.

Parasites de Perciformes dans l'océan Indien.

- *C. guttatii* Khan et Begum, 1971.
- *C. atropusi* Bashirullah et Khan, 1973.
- *C. dollfusi* Bashirullah et Khan, 1973.
- *C. chauhani* Srivastava et Gupta, 1977.
- *C. therapsi* Srivastava et Gupta, 1977.

b — Parasites d'Amphibiens.

α . Nombre des crêtes longitudinales de la capsule buccale de 9 à 12. Petites dents généralement présentes antérieurement entre les crêtes. Vulve pré-équatoriale. Parasites de Ranidae et Bufonidae aux Indes.

- *C. nigrescens* (Linstow, 1906).
- *C. baylisi* Karve, 1930.
- *C. ranae* Khera, 1954 ; espèce redécrite par DESHMUKH, 1969.
- *C. bufonis* Agrawal, 1967.
- *C. cynophylectis* Sahay, 1966.
- *C. tigrinis* Johnson, 1969.

β . Nombre des crêtes longitudinales de la capsule buccale supérieur à 12.

Parasites de Ranidae, Dicroglossidae et Pipadidae en Afrique.

- Vulve pré-équatoriale.

Espèces de grande taille.

- *C. multiruga* Walton, 1932.
- *C. dimitrovi* Durette-Desset et Batcharov, 1974.

- Vulve post-équatoriale.

Espèces de très petite taille.

- *C. kaapstadi* Southwell et Kirsehner, 1937 (= *C. sp.* Kung, 1948).
- *C. mazabukae* Kung, 1948.
- *C. johni* Yeh, 1960.

Parasite de Ranidae en Amérique du Nord.

- *C. multilineatus* Kung, 1948.

III. Genre *Oncophora* Diesing, 1851 (= *Piscilania* Yeh, 1960).

Genre caractérisé par les crêtes longitudinales de la capsule buccale divisées en un groupe antérieur de crêtes nombreuses et serrées et un groupe postérieur constitué par des crêtes courtes et peu nombreuses ou par des rangées d'épines. Tridents présents, à manche très allongé. Corps de la femelle mûre brusquement élargi en arrière de la vulve. 7 paires de papilles pré-cloacales. Parasites de Scobruidae dans l'océan Atlantique et en Méditerranée.

— *O. melanocephala* (Rudolphi, 1819) (= *O. neglecta* Diesing, 1851 ; = *Trichocephalus gibbosus* Rudolphi, 1819) ; espèce redécrite par TÖRNQUIST, 1931.

— *O. albacarensis* Baudin-Laurençin, 1972 (= *O. melanocephala* sensu Baudin-Laurençin, 1970, nec *O. melanocephala* (Rudolphi, 1819)).

IV. Genre *Serpinema* Yeh, 1960.

Genre caractérisé par les crêtes longitudinales de la capsule buccale séparées en un groupe ventral et un groupe dorsal. Tridents présents. Vulve à lèvre antérieure souvent proéminente. 6 à 7 paires de papilles pré-cloacales. Spicule droit souvent coudé ou muni d'un éperon à son extrémité postérieure. Parasites de Chéloniens.

A. Valves de la capsule buccale dépourvues antérieurement de petites crêtes courtes entre les deux groupes dorsal et ventral. Parasites d'Emydidae et de Trionychidae de l'Ancien Monde.

Parasites d'Emydidae dans la région paléarctique.

— *S. microcephalus* (Dujardin, 1845)¹ ; espèce décrite récemment par SEURAT, 1915, TÖRNQUIST, 1931, et SHARPILO, 1976.

Parasites d'Emydidae et de Trionychidae en Asie.

- *S. kachugae* (Baylis et Daubney, 1922).
- *S. intermedius* (Hsü et Hoeppli, 1931).
- *S. octorugatus* (Baylis, 1933) ; l'espèce est signalée en Australie par STROMBERG et CRITES, 1973.
- *S. lissemysus* (Gupta et Singh, 1959).

1. Pour la liste des synonymes de *S. microcephalus*, voir TÖRNQUIST, 1931.

B. Valves de la capsule buccale munies antérieurement de quelques petites crêtes courtes entre les deux groupes dorsal et ventral. Parasites de Chéloniens du Nouveau Monde.

1. Valves de la capsule buccale dépourvues en leur milieu de pièces chitinoïdes en forme de croissants. Parasites de Cryptodires (Emydidae et Kinosternidae) en Amérique du Nord et en Amérique du Sud.

— *S. trispinosa* (Leidy, 1852) (= *Camallanus pipientis* Walton, 1935, d'après BAKER, 1979)¹; espèce récemment redécrite par BARUS et MORAVEC, 1967.

— *S. magathi* (Sprehm, 1932).

— *S. parvus* (Caballero, 1939); mise en synonymie avec *S. magathi* par YEH, 1960.

— *S. magnorugosus* (Caballero, 1939).

2. Valves de la capsule buccale pourvues en leur milieu de pièces chitinoïdes en forme de croissants. Parasites de Pleurodires (Pelomedusidae) en Amérique du Sud.

— *S. amazonicus* (Ribeiro, 1940).

C. Espèces non classées parce que insuffisamment décrites.

— *S. ptychozoondis* (Mac Callum, 1918), parasite de Geckonidae à Java.

— *S. undulatus* (Railliet et Henry, 1915) (= *Cucullanus viviparus* sensu Linstow, 1906, nec Bloch, 1782), parasite d'Emydidae et de Kinosternidae au Muséum de Königsberg.

V. Genre *Camallanides* Baylis et Daubney, 1922.

Genre caractérisé par les valves de la capsule buccale pourvues en leur milieu d'un épaissement longitudinal externe. Crêtes longitudinales au nombre de 12 à 14, peu marquées. Tridents transformés en baguettes simples. Vulve pré-équatoriale, située au sommet d'un appendice tubulaire. Gubernaculum présent. Spicule droit ailé, souvent coudé à son extrémité distale. 5 à 7 paires de papilles pré-cloacales. Parasites de Colubridae et Elapidae en Asie tropicale.

— *C. prashadi* Baylis et Daubney, 1922; redécrite par AGRAWAL, 1967.

— *C. ptyas* Khera, 1954.

— *C. piscatori* Khera, 1954.

— *C. dhamini* Deshmukh, 1968.

— *C. sp.* Gupta, 1959².

VI. Espèces non classées.

Les espèces suivantes sont difficiles à placer dans l'un ou l'autre des genres précédents parce que insuffisamment décrites :

— *Paracamallanus ophiocephali* Karve, 1941, parasite de Channidae aux Indes. YEH (1960) met cette espèce en synonymie avec *Zeylanema sweeti*; cependant, l'espèce n'est connue que par les femelles et seule une vue médiane de la capsule buccale est donnée par l'auteur; il est donc difficile de juger de la valeur de cette synonymie et même de l'appartenance de l'espèce au genre *Paracamallanus*: KARVE décrit en effet un anneau chitinoïde basal distinct de l'arrière-cavité

1. Pour la liste complète des synonymes de *S. trispinosa*, voir BARUS et MORAVEC, 1967.

2. L'espèce *Camallanides bungari* (Mac Callum, 1918) est en réalité un Kalicéphale (voir CHITWOOD, 1932).

buccale, alors que chez les *Paracamallanus* l'arrière-cavité correspond à l'anneau chitinoïde des *Camallanus*. Notons que cette espèce ne doit pas être confondue avec l'espèce *Paracamallanus ophicephali* (Pearse, 1933).

— *Paracamallanus theraponis* Kalyankar, 1971, parasite de Serranidae aux Indes. KALYANKAR a placé cette espèce dans le genre *Paracamallanus* en raison d'un septum qui divise la capsule buccale en deux parties ; cependant, la figure montre qu'il existe indépendamment de ce septum, un anneau chitinoïde basal ; comme dans le cas précédent, l'appartenance de l'espèce au genre *Paracamallanus* est donc très discutable.

— *Neocamallanus ophicephali* Rehana et Bilqees, 1972, parasite de Channidae et de Siluridae aux Indes. Il est difficile d'après les figures d'évaluer la hauteur de l'arrière-cavité buccale de cette espèce, et donc de la placer dans l'un des genres *Paracamallanus* ou *Camallanus* ; s'il s'agit d'une espèce distincte, elle devra être renommée, le terme *ophiocephali* étant pré-occupé.

— *Camallanides hemidenta* Majumdar, 1965, parasite de Channidae aux Indes. MAJUMDAR attribue cette espèce au genre *Camallanides* à cause de la présence de « reduced rod-like tridents » ; cependant, elle ne présente pas les principaux caractères de ce genre, et les « reduced rod-like tridents » doivent correspondre en réalité aux ébauches de tridents que l'on rencontre chez certains *Camallanus* et *Paracamallanus*, et non aux baguettes des *Camallanides* ; l'espèce appartient donc vraisemblablement à l'un des deux genres précédents.

Les espèces *Neozeylanema bhli* Sinha et Sahay, 1966 (signalées sous presse par SAHAY et NARAYAN, 1967) et *Zeylanema yehia*, *Z. bidigitalis* et *Z. tridensis* Bashirullah, 1970, n'ont à notre connaissance pas été décrites.

Nous n'avons pu nous procurer la description des espèces *Neocamallanus vachii* Wahid, 1969, *Neocamallanus apapillata* Ghosh et Majumdar, 1972, et *Camallanus aotea*, *C. kububudgeri* et *C. guubuyumbu* Slankis et Korotaeva, 1974.

ANALYSE DES CARACTÈRES

I. Capsules buccales

A. La valeur phylogénique de la présence d'une arrière-cavité buccale a été mise en évidence par CAMPANA-ROUGET (1961) : le genre *Paracamallanus*, muni d'une arrière-cavité buccale comme les 3^e stades larvaires du genre *Camallanus*, est le plus primitif.

L'arrière-cavité se réduit progressivement chez les espèces parasites de Poissons d'eau douce indo-malais, Clariidae et Siluridae, Channidae, Anabantidae et Mastacembelidae, où l'on rencontre tous les intermédiaires entre les genres *Paracamallanus* et *Camallanus*.

Les espèces considérées comme les plus évoluées sont celles où l'arrière-cavité est réduite à un mince anneau chitinoïde, ce que l'on rencontre chez les *Camallanus* de Cypriniformes et d'Amphibiens en Asie tropicale, chez les *Camallanus* de Poissons d'eau douce des autres régions et chez ceux de Poissons marins.

B. La présence de denticulations sur les crêtes longitudinales de la capsule se rencontre le long d'un ou deux petits rameaux évolutifs qui se sont différenciés chez les Poissons d'eau douce indo-malais.

C. Le nombre des crêtes longitudinales augmente au cours de l'évolution : il est en effet de 9 à 11 chez la majorité des *Paracamallanus* et des *Camallanus* de Poissons d'eau douce indo-malais, alors qu'il est toujours supérieur à 12 et atteint quelquefois 30 à 40 chez les *Camallanus* de Cypriniformes et de Poissons marins qui, nous l'avons vu plus haut, sont considérés comme les plus évolués.

D. En règle générale, les tridents s'allongent au cours de l'évolution ; chez plusieurs petits rameaux évolutifs qui se sont développés en Asie tropicale, ils ont au contraire tendance à s'atrophier et à disparaître en fin de lignée.

2. Papilles caudales mâles

A. Le nombre des papilles pré-cloacales paraît avoir une signification évolutive, mais contrairement à ce qui se passe chez les Procammallaninae, il augmente avec le degré d'évolution : il est en effet en grosse majorité de 5 paires dans le genre primitif *Paracammallanus*, alors que chez la plupart des espèces appartenant aux genres plus évolués *Camallanus*, *Serpinema* et *Oncophora*, il est de 6 à 7 paires ; les 4 espèces de *Camallanus* où il est de 5 paires sont précisément celles qui par le développement de leur anneau chitinoïde basal sont proches des *Paracammallanus*.

B. La présence de deux paires ad-cloacales ventrales semble un caractère définitivement fixé chez les Camallaninae ; il est signalé chez la plupart des espèces et doit vraisemblablement exister chez toutes.

C. Le nombre des papilles post-cloacales est le plus souvent de 5 à 6 paires ; les trois paires les plus proches du cloaque peuvent être groupées, mais ce caractère, s'il est particulièrement fréquent chez les *Camallanus* parasites d'Amphibiens, se rencontre dans toutes les lignées.

3. Spicules

A. La taille des spicules et le spicule-ratio sont très variables dans une même lignée suivant les espèces et même à l'intérieur d'une même espèce suivant les individus ; de même, on observe dans toutes les lignées et à tous les niveaux évolutifs une tendance à la disparition du spicule gauche.

B. Une tendance à la formation d'un éperon ou d'un coude à l'extrémité distale du spicule droit semble accompagner l'adaptation aux Tétrapodes. Ce caractère ne se rencontre que chez 2 espèces parasites de Poissons, alors qu'il est signalé chez 9 espèces de *Camallanus* sur les 17 qui sont parasites d'Amphibiens, chez 5 espèces sur 9 de *Serpinema* (parasites de Tortues), et 2 espèces de *Camallanides* (parasites d'Ophidiens) sur les 4 où les mâles sont connus.

4. Position et forme de la vulve

A. La vulve est en général située dans la région médiane du corps ; elle peut montrer suivant les lignées une tendance à devenir pré ou postéquatoriale : ainsi elle est souvent pré-équatoriale chez les *Camallanus* parasites de Poissons marins, alors qu'elle a tendance à devenir postérieure chez les parasites de Cypriniformes asiatiques.

B. On observe une modification des lèvres vulvaires dans le genre *Serpinema*, où la lèvre antérieure se développe énormément chez plusieurs espèces, et dans le genre *Camallanides*, où la vulve s'ouvre à l'extrémité d'un appendice tubulaire.

5. Longueur de la queue chez la femelle

La queue chez la femelle est, dans l'ensemble des Camallaninae, relativement courte ; elle s'allonge dans la lignée des *Camallanus* parasites de Cypriniformes.

CONCLUSIONS PALÉOBIOGÉOGRAPHIQUES

Nous pouvons tirer de l'étude précédente les conclusions suivantes sur la paléobiogéographie de la sous-famille (schématisées sur les figures 1 et 2) ; ces conclusions basées sur des éléments morphologiques précisent les hypothèses qui avaient été émises par STROMBERG et CRITES en 1973.

1. En ce qui concerne les parasites de Poissons :

— Les formes les plus primitives (genre *Paracamallanus*) se rencontrent principalement en Asie tropicale, d'une part chez les Siluriformes (Clariidae et Siluridae), d'autre part chez les Channiformes. C'est également dans cette région que l'on rencontre les *Camallanus* les plus primitifs, chez les Channiformes et les Perciformes des familles Mastaembelidae et Anabantidae. On y rencontre par ailleurs une grande variété de formes constituant un ensemble de petits rameaux évolutifs divergents.

Les formes de *Camallanus* sud-asiatiques les plus évoluées se rencontrent dans deux groupes : d'une part chez les Cypriniformes, où elles constituent une lignée évolutive caractérisée principalement par l'allongement de la queue chez la femelle, d'autre part chez les Poissons de mer dans les océans Indien et Pacifique.

Les Camallaninae ont donc dû prendre naissance chez les Siluriformes dans la région indo-malaise, à partir d'un ancêtre Procammallaninae, et se sont diversifiés au moment du développement des Channiformes et des Anabantidae et Mastaembelidae. Ultérieurement une lignée s'est individualisée chez les Cypriniformes, tandis qu'une autre lignée s'adaptait aux Poissons de mer.

— Le genre *Oncophora* est vraisemblablement issu de cette dernière lignée et a subi une rapide évolution en s'adaptant aux Scombridae et en se répandant dans toutes les mers.

— Dans le nord de l'Asie et en Amérique du Nord, les *Camallanus* sont représentés par quelques espèces peu spécifiques, qui sont des espèces évoluées appartenant par la longueur de la queue à la lignée parasite de Cypriniformes ; ils ont donc dû parvenir dans ces régions avec ceux-ci, et se sont ensuite adaptés aux autres groupes de Poissons d'eau douce.

— Les deux espèces européennes peuvent également se rattacher morphologiquement à la lignée parasite de Cypriniformes ; elles sont donc vraisemblablement issues comme les espèces nord-asiatiques et nord-américaines d'espèces parasites de Cyprinidae venant d'Asie.

— En Amérique du Sud, le genre *Camallanus* n'est représenté que par une espèce parasite d'Ostéoglossiforme ; cette espèce est peu connue et le mâle en particulier n'a pas été décrit ; elle est cependant de type évolué par le grand nombre des crêtes de la capsule buccale ; elle est donc issue soit des espèces nord-américaines soit des espèces marines, dont elle se rapprocherait plutôt par sa queue courte.

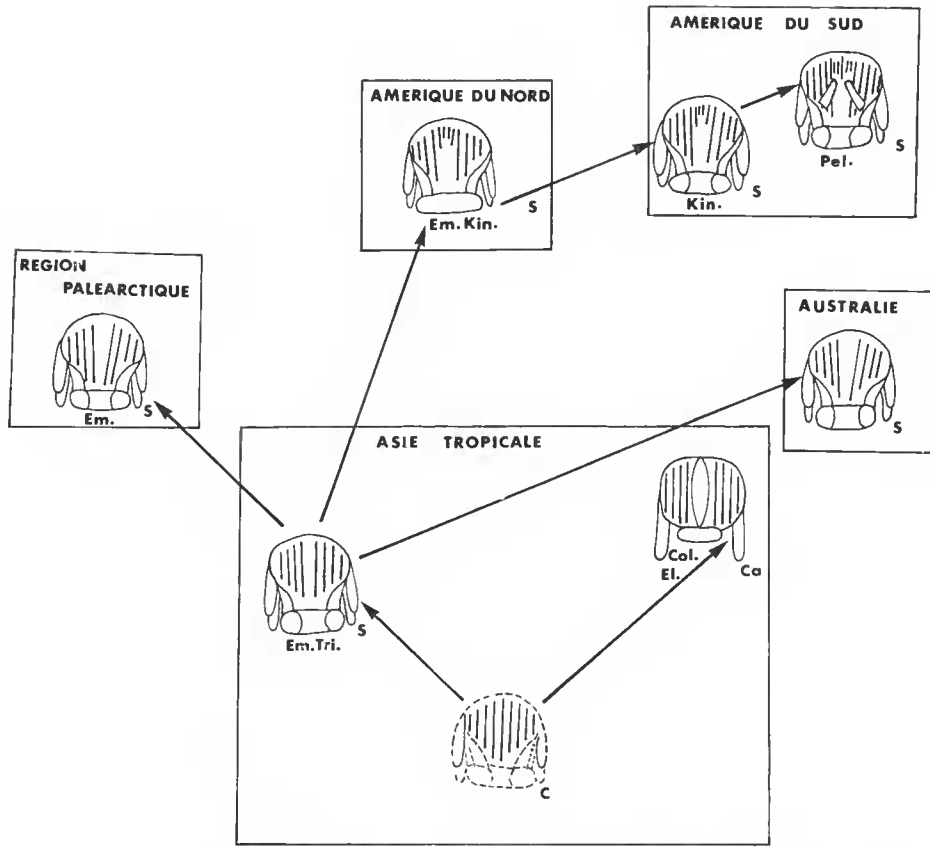


FIG. 2. — Schéma représentant l'évolution des Camallaninae parasites de Reptiles (genres *Serpinema* et *Camallanides*).

C. : ancêtre *Camallanus* parasite de Poissons ; S : genre *Serpinema* ; Ca : genre *Camallanides* ; Em. : Emydidae ; Tri. : Trionychidae ; Kin. : Kinosternidae ; Pel. : Pelomedusidae ; Col. : Colubridae ; El. : Elapidae.

— En Afrique, la faune de Camallaninae représente une image appauvrie de la faune indo-malaise : elle est constituée de quelques formes soit primitives soit évoluées, qui sont toutes voisines de formes rencontrées en Indo-Malaisie chez des hôtes de mêmes familles ; elles ont donc été introduites en même temps que ces hôtes, au moment de la colonisation de l'Afrique par des Poissons venant d'Asie tropicale.

2. L'adaptation des *Camallanus* aux Amphibiens a dû s'effectuer chez les Ranidae et les Bufonidae dans la région indo-malaise, où l'on rencontre les formes dont la capsule buccale a le plus petit nombre de crêtes.

En se basant principalement sur la présence fréquente chez les *Camallanus* d'Amphibiens d'un spicule droit coudé, DURETTE-DESSERT et BATCHAROV (1974) concluent qu'ils forment un groupe distinct de celui des *Camallanus* de Poissons. Nous ne pensons cependant

pas que ce caractère permette de conclure au monophylétisme des *Camallanus* d'Amphibiens car, au moins dans la région indo-malaise, ils appartiennent à deux lignées, l'une à crêtes de la capsule denticulées et l'autre à crêtes lisses.

Les *Camallanus* de cette dernière lignée ont dû se disperser avec leurs hôtes depuis la région indo-malaise jusqu'en Afrique et en Amérique du Nord.

En Afrique, à côté de deux espèces de grande taille, on rencontre trois espèces qui, par leur très petite taille et leur queue terminée par de nombreuses pointes chez la femelle, présentent une convergence avec les *Procamallanus* et les *Spirocamallanus* d'Amphibiens africains ; ces caractères qui rappellent des caractères larvaires nous paraissent l'indice d'une capture récente, à partir soit des *Camallanus* des autres Amphibiens, soit des *Camallanus* de Poissons.

3. L'adaptation aux Emydidae, donnant le genre *Serpinema* doit être antérieure à la dispersion de ces hôtes puisque l'on retrouve des représentants du genre dans les différentes régions où les Emydidae se sont répandues.

4. Par contre, l'adaptation aux Colubridae donnant le genre *Camallanides* doit être postérieure à la dispersion de ces hôtes car le genre n'est présent que chez les Colubridae indo-malais ; le genre présente des caractères spécialisés qui l'isolent des autres genres et supposent une évolution rapide, comme cela se produit lors d'une adaptation à des hôtes très différents des hôtes d'origine.

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